# THE ORDOVICIAN TRILOBITE FAUNAS OF THE BUILTH-LLANDRINDOD INLIER, CENTRAL WALES. PART II. 

By CHRISTOPHER PAUL HUGHES

## CONTENTS

Page
I. Terminology ..... 117
II. Definition of measurements ..... 118
III. Systematic descriptions ..... II9
Family Trinucleidae Hawle \& Corda ..... 119
Subfamily Trinucleinae Hawle \& Corda ..... 121
Trinucleus fimbriatus Murchison ..... 122
Trinucleus abruptus sp. nov. ..... 132
Trinucleus cf. acutofinalis Whittard. ..... 137
Anebolithus sp. ..... I39
Bergamia prima (Elles) ..... 140
Bergamia whittardi sp. nov ..... 146
Trinucleinid gen. et sp. indet. ..... 151
Subfamily Cryptolithinae Angelin ..... 152
Cryptolithus instabilis sp. nov. ..... 152
Cryptolithus sp. A. ..... 157
?Cryptolithus sp. B. ..... 157
?Cryptolithus sp. C. ..... 158
Bettonia chamberlaini (Elles) ..... 159
Bettonia aff. superstes Whittard ..... 167
Subfamily Marrolithinae subfam. nov. ..... 167
Marrolithus sp. ..... 168
Protolloydolithus reticulatus (Elles) ..... 169
Telaeomarrolithus intermedius sp. nov. ..... 174
Telaeomarrolithus vadiatus (Murchison) ..... 178
IV. Acknowledgements ..... 179
V. References ..... 179

## SYNOPSIS

This paper is the second in a series of four dealing with the Ordovician trilobite faunas of the Builth-Llandrindod Inlier. Those described belong to eight genera and seventeen species, of which four are new. They comprise three subfamilies of the family Trinucleidae. The Marrolithinae is a new subfamily.

## I. TERMINOLOGY

The terminology adopted here is that in standard use for trinucleids, with the addition of the following two terms. The term 'arc' is used instead of 'concentric row' as previously proposed (Hughes 1970), and the term 'inter-radial ridge' is used for the ridges separating adjacent rows of pits on the fringe.

## II. DEFINITION OF MEASUREMENTS

As in part I of this study (Hughes 1969), the single orientation method of measurement proposed by Shaw (1957) has been followed. In those measurements involving distances between, or to, furrows, the measurements have been taken from the deepest (dorsoventrally) point in the furrow. All measurements are taken from internal moulds except where specifically stated to the contrary.

Measurements taken on trinucleids (see Text-fig. I).
A preoccipital cephalic length-measured in the sagittal line from the occipital furrow to the anterior margin of the cephalon.
$\mathrm{A}_{1}$ cephalic length-measured in the sagittal line from the posterior margin of the occipital ring to the anterior margin of the cephalon. If an occipital spine is present, then the measurement is taken from the posterior tip of the spine.
B glabellar length-measured in the sagittal line from the occipital furrow to the anterior of the glabella.
$\mathrm{B}_{1}$ the distance between the posterior lateral glabellar furrows and the anterior of the glabella, as projected onto the sagittal line.
$\mathrm{B}_{2}$ the distance between the median lateral glabellar furrows and the anterior of the glabella, as projected onto the sagittal line.


Fig. i. Diagram showing the measurements taken on trinucleids.
$\mathrm{B}_{3}$ the distance between the anterior lateral glabellar furrows and the anterior of the glabella, as projected onto the sagittal line.
$\mathrm{B}_{4}$ the distance between the median glabellar node and the anterior of the glabella, measured in the sagittal line.
I cephalic width-measured in a transverse direction along the posterior margin of the cephalon.
$I_{1}$ maximum cephalic width excluding fringe--measured in a transverse direction.
K maximum glabellar width-measured in a transverse direction between the axial furrows.
$\mathrm{K}_{1}$ posterior glabellar width-measured in a transverse direction across the occiput.
$\mathrm{R}_{1}$ maximum thoracic width-measured in a transverse direction.
$R_{2}$ anterior thoracic axial width-measured in a transverse direction along the anterior thoracic margin between the axial furrows.
Q thoracic length-measured in the sagittal line.
Q1 anterior thoracic segment length-measured in the sagittal line. maximum pygidial width-measured in a transverse direction. anterior pygidial axial width-measured in a transverse direction. pygidial length-measured in the sagittal line between the articulating furrow and the inner margin of the posterior border.

## III. SYSTEMATIC DESCRIPTIONS

Family TRINUCLEIDAE Hawle \& Corda, 1847
In this study the need for the revision of the subfamilial classification of the trinucleids became apparent and this question is to be dealt with fully elsewhere. For convenience of reference and comparison diagnoses of the subfamilies and genera described in this paper are given below. The subfamily Marrolithinae nov. is here erected for those genera thought to be closely related to Marrolithus, but placed in the Cryptolithinae by Whittington (in Moore 1959), i.e. Marrolithus, Cryptolithoides, Marrolithoides, Protolloydolithus, Reuscholithus, Telaeomarrolithus together with Costonia.

## Subfamily TRINUCLEINAE Hawle \& Corda, 1847

Diagnosis. Cephalon semi-circular; glabella with three pairs of lateral glabellar furrows; pseudofrontal lobe generally prominent; alae may be developed; occipital spine absent; eye tubercles and ridges absent. Fringe with pits of upper lamella sunk into radial sulci; variable number of arcs present external to the girder.

Genus TRINUCLEUS Murchison, I839
Diagnosis. Trinucleinids having one E arc and variable number of I arcs; glabella clavate with prominent pseudofrontal lobe. Pygidium much broader than long, generally with furrowed pleural fields.

## Genus ANEBOLITHUS Hughes \& Wright, 1970

Diagnosis. Trinucleinids with no E arcs, $\mathrm{I}_{1}$ and $\mathrm{I}_{2}$ complete $\mathrm{I}_{3}$ variably developed. Glabella pyriform with pseudofrontal lobe; median glabellar node present. Pygidium much wider than long, anterior part of pleural fields faintly furrowed.

## Genus BERGAMIA Whittard, 1955

Diagnosis. Trinucleinids having $\mathrm{E}_{1}$ fully and $\mathrm{E}_{2}$ variably developed; up to six I arcs present laterally; glabella clavate with prominent pseudofrontal lobe; median glabellar node present. Pygidium short, pleural fields furrowed.

## Subfamily CRYPTOLITHINAE Angelin, 1854

Diagnosis. Cephalon generally semi-circular; glabella clavate to carinate; up to three weakly developed lateral glabellar furrows; occipital node generally present though may be small, absent in Eirelithus; alae, eye tubercles and ridges generally absent in adult form. Fringe with one arc external to girder in early genera, more arcs present in later forms; except in early genera, pits generally arranged radially; concentric ridges between arcs on upper lamella common.

## Genus CRYPTOLITHUS Green, 1832

Diagnosis. Cryptolithinid with $\mathrm{E}_{1}$ and up to three I arcs continuous medially, variable number of further I arcs developed laterally; pits of upper lamella arranged radially medially but may be irregular laterally due to adventitious pits; $\mathrm{E}_{1}$ and $I_{1}$ pits generally larger than the remainder; concentric ridges between arcs on upper lamella common. Glabella clavate with three pairs of weak lateral glabellar furrows. Pygidium wider than long; pleural fields generally furrowed.

## Genus Bettonia Whittard, 1956

Diagnosis. As for Cryptolithus except that a variable number of adventitious pits may be developed medially and posterolaterally external to $\mathrm{E}_{1}$.

Subfamily MARROLITHINAE subfam. nov.
Diagnosis. Cephalon generally with angulate margin anterolaterally; glabella pyriform, rarely with swollen pseudofrontal lobe; occipital spine may or may not be developed. Fringe typically swollen anterolaterally except in early genera; one arc developed external to the girder except in later genera in which two are developed; pits may or may not be radially arranged, if so may be set in sulci.

## Genus MARROLITHUS Bancroft, 1929

Diagnosis. Marrolithinid with one E and a variable number of I arcs; fringe sharply angulated anterolaterally with variable inflation and pit enlargement. Glabella pyriform with one to three pairs of generally weakly developed lateral glabellar furrows. Pygidium wider than long, pleural fields usually weakly furrowed or smooth.

## Genus PROTOLLO YDOLITHUS Williams, 1948

Diagnosis. Marrolithinid with regular $\mathrm{E}_{1}$ and $\mathrm{I}_{1}$ arcs and numerous smaller irregularly arranged pits internal to $I_{1} ; E_{1}$ and $I_{1}$ separated by a sharp ridge on upper lamella; anterolateral corners rounded; no swelling or inflation of pits. Glabella elongate with three pairs of weak lateral glabellar furrows; short preglabellar field developed. Pygidium wider than long, pleural fields generally strongly furrowed.

## Genus TELAEOMARROLITHUS Williams, 1948

Diagnosis. Marrolithinid with only one complete E arc but up to eleven I arcs present anterolaterally; occasional pits of $E_{2}$ may be developed anterolaterally; anterolateral corner angulate; lower lamella may be inflated anterolaterally with pits of $\mathrm{E}_{1}$ enlarged; upper lamella with pits in sulci except in inner regions laterally. Glabella pyriform with weakly developed pseudofrontal lobe; three pairs of lateral glabellar furrows developed.

## Subfamily TRINUCLEINAE Hawle and Corda, 1847

Genus TRINUCLEUS Murchison, 1839
1927 Botriodes Stetson.
1950 Edgellia Shaw in Shaw and Stubblefield.
Diagnosis. See above (page irg).
Type Species. Trinucleus fimbriatus Murchison 1839.
Distribution. Arenig to basal Caradoc of the British Isles, Norway and Sweden; Middle Ordovician of Russia. Type species from the basal Caradoc of Wales.
Discussion. There has been considerable debate, both in the early part of the century and again in the 1950's, over the validity of the generic name Trinucleus Murchison 1839 and its type species. The early discussion, conducted chiefly by Foerste (1910: 10) and Raymond (1913:4; 1913a:26-30) centred around whether Cryptolithus Green 1832 should have priority over Trinucleus. Subsequent work however, has shown the two genera to be distinct. Shaw in Shaw and Stubblefield (1950: 624), like Raymond (1913: 4), considered 'Trinucleus' caractaci Murchison
to be the type-species of Trinucleus and erected Edgellia for what became, as a result of his selection, the generically unplaced fimbriatus. However they had overlooked the selection by Vogdes (I890: 84) of T. fimbriatus as the type-species of Trinucleus. In March 1958 the ICZN opinion 505 was published validating Trinucleus Murchison 1839 non Link 1807, with Trinucleus fimbriatus Murchison r839 as type species.

Størmer (1930: I3) showed the genus Botrioides Stetson, 1927 to be synonymous with Trinucleus Murchison.

## Trinucleus fimbriatus Murchison, 1839

(Pl. I, figs $\mathrm{I}-9$; Pl. 2, figs $\mathrm{I}-\mathrm{I} 4$; Pl. 3, fig. I; Text-figs 2, 3)
1839 Trinucleus fimbriatus Murchison: 660, pl. 23, figs 2a, b.
1851 Tretaspis fimbriatus (Murchison); Sedgwick and M'Coy: pars, 146, non pl. IE, figs 16, 16 a .
1853 Tretaspis fimbriatus (Murchison); Salter: 3, 5, 8.
1890 Tvinucleus fimbriatus Murchison; Vogdes: 84.
1912 Tvinucleus fimbriatus Murchison; Reed: 349, 351-352, 385, 390, pl. 18, fig. 10, pl. 19, figs $2,2 a$.
1913 Trinucleus fimbriatus Murchison; Raymond: 4.
1913a Trinucleus fimbriatus Murchison; Raymond: 28-30.
1914 Trinucleus fimbriatus Murchison; Reed: pars, 350-352, 354, pl. 28, fig. 2, non figs 1, 3.
1925 Trinucleus fimbriatus Murchison; Raymond: 19-21.
1927 Trinucleus fimbriatus Murchison; Stetson: 87-88, 96, fig. 5.
1930 Trinucleus fimbriatus Murchison; Størmer: 14, 30, 36, 75.
1940 Trinucleus fimbriatus Murchison; Elles: pars, 415-419, 421, 424, 432, pl. 30, fig. 6.
1940 Trinucleus fimbriatus mut. ultinus Elles: 416-419, 421, 424-425, 432, pl. 30, figs 7, 8.
1940 Trinucleoides salteri Elles: 428, pl. 30, fig. 9.
1941 Trinucleus fimbriatus Murchison; Whittington: 22, 23, 26.
1941 Trinucleoides salteri Elles; Lamont: 443-444.
1948 Trinucleus fimbriatus Murchison; Williams: 85.
1948 Trinucleus fimbriatus Murchison; Lamont: 376-379, fig. A.
1950 Edgellia fimbriatus (Murchison); Shaw in Shaw and Stubblefield: 624-625.
1956 Trinucleus fimbriatus Murchison; Stubblefield and Whittington: 49-54.
1956 Trinucleus fimbriatus Murchison; Whittard: 45, 46, 48, 65, pl. 6, fig. 4.
Diagnosis. Trinucleus with arcs $\mathrm{I}_{1-5}$ generally developed; $\mathrm{E}_{1}$ and $\mathrm{I}_{1}$ pits larger than remainder; $I_{5}$ rarely present medially; inter-radial ridges angulate. Pygidium triangular with between six and nine axial rings; pleural fields generally with six ribs. It should be noted that the figure of the species given in Moore (1959: fig. 323.5) is incorrect both in the distribution of the pits on the fringe and in the characters of the pygidium.

Lectotype. GSM Geol. Soc. Coll. 6836a. (Pl. 2, fig. 2). External mould of cranidium.

Dimensions. Although the lectotype is poorly preserved the following approximate measurements give some indication of its dimensions.

| A | I |
| :---: | :---: |
| $8 \cdot 0$ | $20 \cdot 0$ |

Both measurements in mm. For explanation of symbols see Text-fig. I.
Type locality and horizon. Dark shales in the Gwern-yfed-fâch quarry half a mile south-east of Builth Road station of basal Caradoc age (gracilis Zone).

Other figured material. It. 27 I9 (Pl. 2, fig. 4) ; It. 2720 (Pl. 2, fig. I3) ; It. 2721 (Pl. 2, fig. 6) ; It. 2722 (Pl. I, fig. 6) ; It. 2723 (Pl. 2, fig. I4) ; It. 2724 (Pl. 2, fig. 3) ; It. 2725 (Pl. 2, fig. 8) ; It. 2726 (Pl. I, fig. 3); It. 2727 (Pl. I, fig. 9) ; It. 2728 (Pl. 2, fig. 5) ; It. 2729 (Pl. I, fig. 8) ; It. 2730 (Pl. I, fig. 7, Pl. 2, fig. 12); It. 273 I (Pl. 2, fig. I) ; It. 2732 (Pl. I, fig. 5) ; It. 2733 (Pl. I, fig. 2); It. 2734 (Pl. 2, fig. II); It. 2735 (Pl. I, fig. 4); It. 8798 (Pl. 2, figs 9, ro); BM 59499 (Pl. 2, fig. 7); GSM 35356 (Pl. 3, fig. I); Wattison Collection, H.I2 (Pl. I, fig. I).

Distribution. Known with certainty only from the basal Caradoc of the Builth-Llandrindod region. It may also be present in South Wales but none of the records of the species in the Geological Survey Memoirs for South Wales has been confirmed to date.

Description. The complete individual is roundly rectangular being slightly wider than long, excluding the genal spines.

The cephalon is semi-elliptical and approximately twice as wide as long; large individuals are relatively wider; small ones relatively narrower. Discounting the fringe, the maximum width measured across the genal regions is always slightly over twice the glabellar length, with the larger individuals relatively narrower.

The glabella is clavate, strongly convex and elevated above the genal regions, consisting of a swollen pseudofrontal lobe occupying the anterior two-thirds of the glabella, with a narrow stalk-like posterior portion. In profile it is convex in front and on top, sloping uniformly down to the posterior. Three pairs of lateral glabellar furrows are present. The anterior pair occur as small pit-like depressions on the side of the glabella, slightly posterior to the mid-point of the pseudofrontal lobe (Pl. I, fig. 3). The median pair, marking the rear of the pseudofrontal lobe, consists of elongated ( $t r$.) pits. The posterior furrows are again elongate ( $t r$.) pits directed anteromedially. Both the median and posterior pairs of glabellar furrows are placed on the side of the glabella some distance inside the axial furrows (Pl. I, fig. 4). Lateral and slightly posterior to the posterior lateral glabellar furrows there is commonly a small pit-like depression of uncertain significance, which may represent the outer end of the posterior lateral glabellar furrow (Pl. I, fig. 3). The base of the glabella (Pl. I, fig. 7), behind the posterior lateral glabellar furrows, is slightly swollen to form an occiput which is a little less than half the width of the pseudofrontal lobe, and is bounded posteriorly by the occipital furrow. A small median glabellar node is usually present on the external surface of the glabella approximately opposite the anterior pair of lateral glabellar furrows. Medially the dorsal surface of the glabella bears a coarse reticulation, which may also be present, though much finer, on the frontal slope and sides of the glabella (Pl. I, fig. 7).

The occipital ring is short (sag.), convex posteriorly and with no occipital spine. Deep elongate pits are developed at the lateral ends of the occipital furrow, which is relatively shallow medially. The posterior margin is rounded.

Anteriorly the axial furrows are deep and narrow with prominent fossulae near their anterior extremities (Pl. I, fig. 4). Posteriorly the furrows closely follow the margin of the glabella to about the position of the anterior pair of lateral glabellar furrows; posterior to this the furrows converge slightly and become much wider and shallower (Pl. I, fig. 4).

The genal regions are roundly triangular, the outer margin is strongly convex, the inner margin slightly concave, and the posterior margin more or less straight. The genae are moderately convex, the outer margin being very steep and the inner regions sloping more gently posteromedially. Externally they are covered with a strong reticulate pattern of raised ridges, which is most coarsely developed along a broad band lying between the genal angles and the anterior fossulae (Pl. I, fig. 7). At the genal angles the raised ridges tend to coalesce to form a ridge which cuts across the posterior border furrow to the posterior margin, thus isolating the posterior border furrow from the fringe. No eye tubercle or eye ridges are developed. The posterior border furrow is straight, wide and shallow, terminating in a shallow lateral pit slightly lateral to the fulcrum (Pl. 1, fig. 7). The posterior margin is rounded.

The internal surface of the glabella and the genal regions may show a faint impression of the external reticulate pattern. The lateral pits, and lateral glabellar furrows form raised platforms internally, those of the anterior lateral glabellar furrows commonly being poorly developed; the fossulae form small apodemes. The median glabellar node is rarely discernable on the inside of the glabella. Small apodemes are present ventrally, immediately posterior to the lateral extremities of the occipital ring.

The hypostoma is not known.
In most specimens the fringe has almost certainly undergone some degree of flattening, but it seems most likely that the fringe possessed a gently convex genal roll becoming concave towards the brim. The fringe is of almost uniform width, expanding only slightly towards the genal angles. Six arcs of pits are generally developed, namely $E_{1}$ and $I_{1-5}\left(\mathrm{Pl} . \mathrm{I}\right.$, fig. 4) ; pits of $\mathrm{I}_{6}$ present occasionally. The pits are arranged in deep radial sulci separated by angulate ridges, the pits of $E_{1}$ and $I_{1}$ being larger than the remainder. The radial arrangement of the pits is remarkably persistent, breaking down only at the genal angles.

As has already been shown (Hughes, 1970) half-fringe statistics may safely be used in trinucleid studies without reference to the size of individuals, providing that no early meraspides or protaspides are included. The number of pits in the $\mathrm{E}_{1}$ and $I_{1}$ arcs is generally the same on account of the good radial arrangement and ranges from $18-24$ (half-fringe) with a mode of about 2I (see Tables 1,4 for full details). The number of radial rows developed varies between 12 and 20 (half-fringe) with a mode of $I_{7}$ (see Table 6). Generally arcs $\mathrm{I}_{1-4}$ are present frontally with $\mathrm{I}_{5}$ commencing by row 3 or 4 (see Tables 2, 5).

Slight deformities in the radial pattern of pits are not uncommon. These are usually due to the fusing or bifurcation of an inter-radial ridge giving rise to an incomplete row of pits. Rarely two rows, partial or complete, occur within a single
sulcus, and a further type of irregularity is occasionally seen in the development of an oversize pit in $\mathrm{I}_{2}$ or $\mathrm{I}_{3}$.

Contrary to Reed's belief (1912:385) the pits of the lower lamella do correspond to those of the upper lamella. On the lower lamella shallow sulci are developed however only along the anterior part of the fringe, internal to the girder. The inner part of the lower lamella is convex dorsally and the outer part more or less flat, but directed upwards and outwards from the girder. Commonly the girder is found flattened, obscuring the inner part of the lower lamella and giving a false picture of the pit distribution and shape of the lower lamella. The girder is strong, smooth and merges at the genal angles with the genal spines. These spines are nearly straight, diverge slightly to the rear, have a slight keel on the dorsal side and probably extend for a short distance posterior of the pygidium.

The precise course of the facial suture has not been traced, but by analogy with other trinucleids it is almost certainly marginal, becoming dorsal only at the genal angles, thus leaving the genal spines attached to the lower lamella. Lamont (1948:376) states that on a specimen from the Llanfawr Quarries 'a semi-circular anterior facial suture appears to be present and to run just outside the anterior pits and forward into the fringe so as to enclose a number of pits in the innermost concentric row'. However of the three hundred and fifty cranidia examined from this locality none shows any sign of such a suture. Many do however possess cracks in roughly this position and it is thought that Lamont's 'suture' may well be one of these.
The thorax consists of six segments and is rectangular, being about two and a half times wider than long. The axis, which occupies about one-fifth of the total width, tapers very slightly and is moderately convex. Dorsally the axial furrows are


Fig. 2. Reconstruction of the cephalon of Trinucleus fimbriatus Murchison in dorsal view.
poorly developed, being identified essentially as the line of junction between the convex surface of the axis and the flat surface of the pleurae. Ventrally the furrow is represented by a ridge which appears as a slight depression on internal moulds. The swollen posterior portion of the axis of each segment is separated from the articulating half ring by a wide, shallow articulating furrow, which is deepened laterally into elongate ( $t r$. .) pits which correspond with strong apodemes on the ventral surface. The anterior segment, however, has no articulating half ring developed, but anterior to the normal pair of apodemes a second pair of weakly developed apodemes is present. Small articulatory sockets and processes are developed in the axial furrows, anteriorly and posteriorly respectively, of each thoracic segment, except for the anterior segment which only has the posterior processes. The pleural regions are flat, bluntly terminated, and deflected ventrally and slightly posteriorly at the fulcrum. They are divided into two roughly equal parts by a transversely directed pleural furrow, which is deflected to the posterior at its distal end. The pleurae of the anterior segment are obliquely truncated; the facets being relatively large.

The triangular pygidium is between three and four and a half times wider than long. In general the smaller individuals are relatively wider than the larger. The anterior margin, excluding the articulating half ring, is straight except for the lateral extremities which are deflected slightly to the posterior at a point corresponding to the fulcrum of the posterior thoracic segment. The posterior margin is defined by a slightly raised marginal rim marking the upper limit of the steeply declined posterior border which has, on the external surface, faint, closely spaced terrace lines. The axis is convex, clearly differentiated, and segmented. There may be from six to nine axial rings present, plus a small terminal piece, there being a slight positive correlation between the size of the pygidium and the number of axial rings developed (see Table 9). Anteriorly the axis occupies between about one-fifth and one-seventh of the width of the pygidium and tapers to about one-half this width. The axial furrows are slightly more prominent on the internal moulds than on external moulds, indicating some slight thickening of the exoskeleton along the line of the furrow. Only the anterior axial ring bears apodemes. The pleural fields are gently undulate and are crossed by straight furrows which become progressively more and more posteriorly directed. Each field possesses an anterior border, usually five or six ribs (rarely four or seven, see Table Io), and a small triangular terminal area. Occasional specimens show differing numbers of ribs on the two pleural fields.

The species shows the usual discoidal enrollment characteristic in the trinucleids, with the posterior margin of the pygidium in contact with the inner margin of the lower lamella. Since no articulating half ring is developed on the anterior thoracic segment it is possible that the flexure of the thorax was accommodated between the first and second, and second and third segments to avoid the production of an unprotected lenticular area between the occipital ring and the axis of the anterior thoracic segment (see Whittington, I94Ia: 5IO). Enrolled specimens tend to be too flattened to indicate the relative amounts of flexure between the various segments.

However the first segment generally retains the same orientation as the cephalon, while segments two-six are folded underneath. This suggests that slightly more than half the flexure at least was accommodated by the first two segments; thus on compaction the second segment became inverted with the more posterior thoracic segments and the pygidium (Pl. 2, fig. 6).

Ontogeny. Only one complete meraspis is known, of degree five, but it is reasonable to suppose that isolated cranidia and pygidia smaller than this are also likely to be meraspides. As Barrande (1852: 265) and Whittington (1940: 254; 1959: 447) have recorded, the later meraspides of trinucleids are very similar to the holaspis form; the meraspides of $T$. fimbriatus follow this pattern. Even the smallest specimen (pre-occipital length, $\mathrm{A}=2.2 \mathrm{~mm}$, genal width, $\mathrm{I}_{1}=4.6 \mathrm{~mm}$ ) shows, as far as can be determined, very little difference from holaspides (Pl. 2, fig. I4).
The cephalon in the degree five meraspis ( $\mathrm{A}=5.3 \mathrm{~mm}, \mathrm{I}_{1}=\mathrm{r}_{3} .5 \mathrm{~mm}$ ) (Pl. 2, fig. 8) differs from mature individuals in that the fringe barely reaches posterior of the posterior margin of the cephalon, the posterior margin of the fringe being directed only slightly to the posterior from the genal angle. This is also seen in a slightly larger specimen ( $\mathrm{A}=5.7 \mathrm{~mm}$ ) but a further specimen of the same size shows the typical holaspis form. Thus a pre-occipital length of 5.7 mm may mark the approximate upper size limit of meraspides.

Two specimens ( $\mathrm{A}=3.5 \mathrm{~mm}, 5.0 \mathrm{~mm}$ ) have the posterior margin of the fringe directed transversely and in the smallest specimen known ( $\mathrm{A}=2.2 \mathrm{~mm}, \mathrm{I}_{1}=$ 4.6 mm ) the posterior margin is directed forwards from the genal angles (Text-fig. 3). Further, in these tiny specimens, the anterior lateral glabellar furrows are poorly developed.

All the pygidia which are thought to be of meraspides are very like those of holaspides. Following the general growth pattern found in the holaspides they tend to be relatively wider than the larger individuals. Counts of axial rings and ribs are difficult to make due to their poor definition towards the posterior, but there appears to be six or seven axial rings and about five ribs.

Biometrical data. The following fringe data and bivariate analyses indicate the characteristics of the major features of the dorsal exoskeleton. They also show that there are no significant differences between the sample from the middle quarry, Llanfawr, and the sample from the type locality.

A


B


C

Fig. 3. Diagram illustrating the change in the posterolateral outline of the fringe in meraspides of Trinucleus fimbriatus Murchison with increase in size. c. $\times 4$. A based on It. 2723 (Pl. 2, fig. 14) ; B on It. 2732 (Pl. r, fig. 5) ; C on It. 2725 (Pl. 2, fig. 8).

Although ideally it is considered that the best measurements of size (length, width) of the cephalon would be the cephalic length $\left(\mathrm{A}_{1}\right)$ and the cephalic width (I), it is found, due to slight flattening of the fringe that the glabellar length $(B)$ and the maximum genal width ( $I_{1}$ ) give a more useful indication of size. A general qualitative study of the thorax, combined with the small amount of quantitative data available, indicates that it shows little variation, as is believed the case in most trinucleids. Insufficient data, however, are available to determine if the ratio length to width varies with the overall size of the individual. The sample of pygidia from the middle quarry Llanfawr may include a few specimens of Telaeomarrolithus intermedius sp. nov. (see page 174) or even Marrolithus sp. (see page 168). The effect of any such specimens will, however, be very small since it has proved impossible on qualitative and quantitative grounds to separate differing types of trinucleid pygidia at this locality. Also T. intermedius is very much rarer than T. fimbriatus, and Marrolithus sp. is extremely rare indeed.

Although it is demonstrated below that the sample from Gwern-yfed-fâch does not differ significantly from the much larger sample from Llanfawr, the data from the two samples are not combined, so that further samples may be compared directly with that from the type locality if required.

Fringe Data (half-fringe).
Sample from type locality (Gwern-yfed-fâch).

## Table I

| Number of pits | 21 | 22 | 23 | 24 |
| :--- | :---: | :---: | :---: | :---: |
| $E_{1}$ arc: Number of specimens | 2 | - | - | $I$ |
| $I_{1}$ arc: Number of specimens | $I$ | - | - | $I$ |

Table giving the frequency distribution of the number of pits in the $E_{1}$ and $I_{1}$ arcs (half-fringe) for Trinucleus fimbriatus Murchison from the type locality.

Table 2

|  | row |  |  |  |  |  |  | Number of <br> Specimens |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| $\mathrm{I}_{4}$ | $100 \%$ | - | 3 | 4 | 5 |  |  |  |
| $\mathrm{I}_{5}$ | $33 \frac{1}{3} \%$ | $16 \frac{2}{3} \%$ | $33 \frac{1}{3} \%$ | $16 \frac{2}{3} \%$ | 6 |  |  |  |
| $\mathrm{I}_{6}$ | - | - | - | $100 \%$ | I |  |  |  |

Table showing the percentage of specimens in which a particular inner I arc commences in a given row for Trinucleus fimbriatus Murchison from the type locality.

| TABLE 3 |  |  |  |  |  |
| :--- | ---: | ---: | ---: | ---: | ---: |
| Number of rows | I6 | I7 | I8 | I9 |  |
| Number of specimens | I | I | 4 | I |  |

Table giving the frequency distribution of the number of rows developed (half-fringe) for Trinucleus fimbriatus Murchison from the type locality.
Sample from Middle quarry, Llanfawr, Llandrindod.

TAble 4
$\mathrm{E}_{1}$ arc
$\begin{array}{lllllllllllllll}\text { Number of pits } & \text { I } 8 & 18 \frac{1}{2} & \text { I9 } & \text { I9 } \frac{1}{2} & 20 & 20 \frac{1}{2} & 2 I & 2 I \frac{1}{2} & 22 & 22 \frac{1}{2} & 23 & 23 \frac{1}{2} & 24\end{array}$
$\begin{array}{llllllllllllll}\text { No. of specimens } & 4 & 3 & 4 & 7 & 15 & 9 & 2 I & 7 & 5 & 6 & I & 2 & 2\end{array}$ mean $=20.69 ;$ var. $=1.7650 ; \mathrm{n}=86$
$\mathrm{I}_{1}$ arc
$\begin{array}{lllllllllllllll}\text { Number of pits } & 18 & 18 \frac{1}{2} & \text { I9 } & \text { I } 9 \frac{1}{2} & 20 & 20 \frac{1}{2} & 2 I & 2 I \frac{1}{2} & 22 & 22 \frac{1}{2} & 23 & 23 \frac{1}{2} & 24\end{array}$ $\begin{array}{lllllllllllllll}\text { No. of specimens } & 3 & 2 & 5 & \text { Io } & 15 & 8 & 20 & 8 & 5 & 4 & 2 & 2 & 1\end{array}$ mean $=20.64 ;$ var. $=1.5856 ; n=85$

Table giving the frequency distributions of the number of pits in the $E_{1}$ and $I_{1} \operatorname{arcs}$ (halffringe) for Trinucleus fimbriatus Murchison from the Middle quarry, Llanfawr. Pits occurring on the sagittal line are counted as half pits.

TAble 5

|  | row |  |  |  | Number of <br> Specimens |
| :---: | :---: | :---: | :---: | :---: | :---: |
| $\mathrm{I}_{4}$ | $\mathbf{1}$ | 2 | 3 | 4 | 26 |
| $\mathrm{I}_{5}$ | $96 \%$ | $4 \%$ | - | - | 26 |
| $\mathrm{I}_{6}$ | $25 \%$ | $25 \%$ | $16 \frac{2}{3} \%$ | $33 \frac{1}{3} \%$ | I 2 |
|  | - | - | - | - | - |

Table showing the percentage of specimens in which a particular inner I arc commences in a given row for Trimucleus fimbriatus Murchison from the Middle quarry, Llanfawr.

## Table 6


 mean $=16 \cdot 95 ;$ var. $=-2 \cdot 1678 ; \mathrm{n}=70$
Table giving the frequency distribution of the number of rows developed (half-fringe) for Trinucleus fimbriatus Murchison from the Middle quarry, Llanfawr. Rows situated along the sagittal line are counted as a half row.

Comparison of the number of pits in the $E_{1}$ and $I_{1}$ arcs and also the number of radial rows present for the two samples show no significant differences. The data for the commencement of the inner arcs is also very similar in the two samples; in both virtually all specimens have the $I_{4}$ arc continuous medially, and $50 \%$ of specimens in both cases show $I_{5}$ developed at or before radial row 2 and only rare cases of $I_{6}$ commencing before row 5 . It is thus seen that regarding the major characteristics, the fringe pit distribution is essentially the same in both samples.

Table 7 gives the bivariate statistics for various parameters for both samples. Comparison where possible shows there to be no significant differences between the two samples.

## Table 7

| $\mathrm{x}: \mathrm{y}$ | $\overline{\mathrm{x}}$ | var. x | $\bar{y}$ | var. y | r | $\mathrm{r}_{\mathrm{e}}$ | $\alpha$ | var. $\alpha$ | a | var. a | n |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| $\mathrm{I}_{1}$ : A | 10.95 | 31.3967 | $5 \cdot 85$ | 10.8633 | -. 999 | I $\cdot 000$ | I 09 | 0.0001 | - | - |  |
| $\mathrm{I}_{1}:$ B | $10 \cdot 95$ | 31-3967 | 4.42 | 5.4892 | $0 \cdot 997$ | $0 \cdot 998$ | I. 03 | 0.0025 | 0.42 | 0.00048 |  |
| $\mathrm{B}: \mathrm{K}$ | 4.74 | 4.6130 | $3 \cdot 50$ | $3 \cdot 1900$ | 0.989 | 0.991 | I•II | 0.0075 | 0.83 | $0 \cdot 0049 \mathrm{I}$ |  |
| W: Z | 11.48 | 4.6670 | $3 \cdot 90$ | I 26.200 | 0.979 | 0.982 | I•5I | 0.0270 | - | - | 5 |
| X: 7 | I 80 | $0 \cdot 4089$ | $3 \cdot 8 \mathrm{I}$ | 2.8188 | 0.977 | 0.980 | I-22 | 0.0074 | - | - | 10 |


| I : $\mathrm{A}_{1}$ | 19.27 | 8.8740 | 9.18 | 1.3069 | 0.933 | 0.934 | 0.81 | 0.0076 | - | - | 13 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| $\mathrm{I}_{1}$ : A | 13.55 | $5 \cdot 9093$ | $7 \cdot 84$ | 2.4620 | 0.955 | -. 956 | I. II | 0.0022 | - | - | 51 |
| $\mathrm{I}_{1}: \mathrm{B}$ | 13.81 | $5 \cdot 8768$ | $6 \cdot 02$ | I. 3653 | 0.938 | - .939 | I. 10 | 0.0019 | - | - | 77 |
| A : B | $7 \cdot 83$ | $2 \cdot 2687$ | $5 \cdot 90$ | I. 2516 | 0.983 | 0.984 | 0.99 | 0.0003 | $0 \cdot 74$ | $0 \cdot 00015$ | 122 |
| $B: B_{1}$ | $6 \cdot 08$ | 1.2710 | $4 \cdot 88$ | 0.7859 | 0.977 | 0.978 | 0.98 | $0 \cdot 0002$ | $0 \cdot 79$ | $0 \cdot 00017$ | 168 |
| $\mathrm{B}: \mathrm{B}_{2}$ | 6.05 | I. 2872 | $3 \cdot 91$ | 0.5840 | 0.967 | $0 \cdot 967$ | I $\cdot 04$ | 0.0004 |  | - | 176 |
| $\mathrm{B}: \mathrm{B}_{3}$ | 6.09 | 1.0410 | $2 \cdot 75$ | 0.2487 | 0.923 | $0 \cdot 924$ | I. 08 | $0 \cdot 0012$ | - | - | 140 |
| $\mathrm{B}: \mathrm{K}$ | 6.03 | 1.2344 | $4 \cdot 46$ | 0.7819 | 0.926 | 0.927 | I. 08 | 0.0009 | - | - | 177 |
| $\mathrm{K}: \mathrm{K}_{1}$ | $4 \cdot 46$ | 0.8236 | I. 87 | -.1194 | -. 879 | 0.88I | 0.91 | 0.0013 | - | - | I 44 |
| W: Z | I I 37 | 3.1960 | $3 \cdot 37$ | $0 \cdot 4882$ | 0.949 | 0.950 | I•3I | $0 \cdot 0016$ | - | - | 104 |
| W : X | I I 43 | $3 \cdot 2768$ | $2 \cdot 09$ | o. 1903 | 0.916 | 0.918 | I-3I | 0.0028 | - | - | 98 |
| X : Z | 2.10 | 0.1606 | $3 \cdot 48$ | 0.4381 | 0.860 | 0.862 | I. OO | $0 \cdot 0017$ | I. 65 | 0.00487 | 148 |

Bivariate statistics for Trinucleus fimbriatus Murchison. Upper part of Table for sample from the type locality (Gwern-yfed-fâch) ; lower part for the sample from the middle quarry Llanfawr. All measurements in mm. For explanation of symbols see Text-fig. i.

## Table 8

Thoracic measurements for Tvinucleus fimbriatus Murchison from the middle quarry, Llanfawr. No data available for the type locality. All measurements in mm. For explanation of symbols see Text-fig. I.

## Table 9

| maximum pygidial width in mm | 7.0-11 $\cdot 0$ | II.I-I7.0 |
| :---: | :---: | :---: |
| Number of 6-7 | - | - |
| axial rings 8-9 | 4 | I |
| maximum pygidial width in mm | $7 \cdot 0-11 \cdot 0$ | II $\cdot \mathrm{I}-\mathrm{I} 7 \cdot \mathrm{O}$ |
| Number of 6-7 | II | 4 |
| axial rings 8-9 | 17 | 35 |

$2 \times 2$ tables showing relationship between pygidial size (as measured by width) and number of axial rings, for Trinucleus fimbriatus Murchison. Upper part of table for type locality (Gwern-yfed-fâch) ; lower part for the middle quarry, Llanfawr sample.

## Table io

| Number of ribs on pleural fields | 4 | 5 | 6 | 7 | 8 |
| :--- | ---: | ---: | ---: | ---: | ---: |
| Number of specimens | - | 2 | I | 3 | - |
| Number of ribs on pleural fields | 4 | 5 | 6 | 7 | 8 |
| Number of specimens | 4 | 13 | ro9 | 5 | - |


#### Abstract

Frequency distribution for the number of pleural ribs developed on the pygidium of Trinucleus fimbriatus Murchison. Upper part of table for type locality sample (Gwern-yfed-fâch); lower part for the middle quarry Llanfawr sample.


It may be seen from the above Tables that quantitatively there are no significant differences between the two samples and thus the data from the larger, though non-topotypic sample may be reasonably taken as characterising the species, until such time as more complete data becomes available from the type locality.

Discussion. A difficulty encountered in redescribing this species is the generally poor preservation, particularly of the fringe pits at the type locality, Gwern-yfedfâch. However it has been shown above that the form found at the middle quarry, Llanfawr appears not to differ significantly from that found at the type locality, and the redescription above has been based mainly on the more satisfactory Llanfawr sample.

Elles (1940: 424-425) in describing two new mutations of T. fimbriatus, though on pp. 416, 417 recording T. fimbriatus from Gwern-y-fed Quarry and not from Pencerrig Lake, considered (p. 425) Pencerrig Lake to be the type locality of $T$. fimbriatus Murchison. There is, however, no doubt that the lectotype came from Gwern-yfed-fâch. Although her descriptions were brief she did infer that the fringe of T. fimbriatus mut. ultimus is wider than in the typical form and also that the pits show better radial arrangements at the genal angle. Although she records both the typical form and the ultimus mutation as occurring at Llanfawr, no confirmation has been found for the existence of two varieties at this locality, and all would appear to belong to her ultimus form. However, it has been shown above that the Llanfawr form does not differ from the form occurring at the type locality of T. fimbriatus (Gwern-yfed-fâch); thus Elles's mutation ultimus must be considered as a synonym of $T$. fimbriatus s.s. The present study has also shown that Elles's T. fimbriatus s.s. and mutation primus from Pen-cerig Lake quarry, although dorsally bearing some similarity to T. fimbriatus, possess a lower lamella which clearly shows that two E arcs are present and both are here assigned to the genus Bergamia Whittard, 1955.
T. acutofinalis Whittard, 1956 is readily distinguished by having only three arcs developed internal to the girder; it also differs in that all the pits are of equal size, and the inter-radial ridges are rounded. T. foveolatus (Angelin, 1854) and $T$. foveolatus var. intermedius Størmer, 1930 differ from T. fimbriatus in being much smaller and in having a median ridge developed on the glabella posterior of the
median glabellar node, and also lateral eye tubercles; further the fringe in $T$. foveolatus does not extend behind the posterior margin of the cephalon. T. bronni Sars and Boeck in Boeck, 1838 , is distinguished by its short stubby pygidium with few axial rings and pleural ribs. This last species is very similar to Bergamia, particularly in the characters of the pygidium, although Størmer's figures (1930, Pl. 2, figs $2,5,6,7$ ) show only one $E$ arc and so, for the present at least, it seems better to retain this species in the genus Trinucleus. Trinucleus abruptus sp. nov. (see below) may be easily distinguished by the anterior deflection of the posterior border of the cephalon at the fulcrum, the smaller number of pits in each arc on the fringe and its relatively narrower pygidium with fewer ribs.

Trinucleoides salteri Elles, 1940 is here considered as a junior synonym of Trinucleus fimbriatus Murchison. The single known specimen in the Wyatt-Edgell Collection (GSM 35356, Pl. 3, fig. I) is almost certainly from the basal Caradoc at Gwern-yfed-fâch and is associated with Trinucleus fimbriatus and Cnemidopyge bisecta (Elles) and not with Lloydolithus as claimed by Lamont (194I: 441). Owing to the lower lamella being slightly displaced and pushed up through the upper lamella in places, Elles was misled into believing that the arcs of pits were separated into two series and that tubercles were present laterally. The surface of the glabella and genae is poorly preserved and no trace of any caecae or other surface markings exists. The elongate alae and prominent occipital ring are thought to be accentuated due to distortion on preservation, and the groove between the fringe and left gena to be due to a pygidium folded back beneath the cephalon.

Trinucleus abruptus sp. nov.
(Pl. 3, figs 2-4, 6, 7; Text-fig. 4)
1940 Trinucleus chamberlaini Elles: pars, pl. 29, fig. 13.
1940 Trimucleus cf. foveolatus Angelin; Elles: 425, pl. 31, figs 1-2a.
Diagnosis. Trinucleus with six arcs of pits developed, most probably being $\mathrm{E}_{1}, \mathrm{I}_{1-5}$; fringe of approximately uniform width with posterior border bent forwards external to fulcrum; inter-radial ridges rounded; small median glabellar node; no eye tubercles. Pygidium triangular with segmented axis and faintly ribbed pleural fields.

Type material. Holotype. BM In 36920 (Pl. 3, fig. 7). Internal mould of nearly complete specimen.

Paratypes. BM. In 36921 (Pl. 3, fig. 2) Internal mould of complete specimen. BM 59200 External mould of nearly complete specimen. It. 2736 (Pl. 3, fig. 3) Internal mould of nearly complete specimen. It. 2737 Internal mould of pygidium. It. 2738 (Pl. 3, fig. 6) External mould of cephalon. OUM Bi79 (Pl. 3, fig. 4) Internal mould of nearly complete specimen.

Dimensions.

|  | A | B | $\mathrm{B}_{1}$ | $\mathrm{B}_{2}$ | $\mathrm{B}_{3}$ | I | $\mathrm{I}_{1}$ | K | $\mathrm{K}_{1}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Holotype | $7 \cdot 4$ | $6 \cdot 0$ | $5 \cdot 2$ | $4 \cdot 2$ | $3 \cdot 0$ | 18.8 | 14.2 | $5 \cdot 2$ | $2 \cdot 0$ |
| In 3692I | $8 \cdot 2$ | $7 \cdot 0$ | $5 \cdot 7$ | $4 \cdot 5$ | $3 \cdot 4$ | $20 \cdot 3$ | I5.9 | $5 \cdot 8$ | $2 \cdot 3$ |
| BM 59200 | $6 \cdot 3$ | $5 \cdot 5$ | $4 \cdot 5$ | $3 \cdot 6$ | $2 \cdot 5$ | $15 \cdot 3$ | 12.5 | $4 \cdot 8$ | I. 8 |
| It. 2736 | - | $5 \cdot 8$ | $4 \cdot 6$ | $3 \cdot 5$ | 2.I | - | c. $\mathrm{I} 4 \cdot \mathrm{O}$ | $5 \cdot 0$ | I.9 |
| It. 2738 |  | $4 \cdot 2$ | - | - | - | 13.5 | c. II•I | - |  |
| OUM Bı79 | c. $8 \cdot 0$ | $6 \cdot 6$ | - | - | - | I 8.8 | 14.6 | $5 \cdot 5$ |  |


| Holotype | $\begin{gathered} \mathrm{R}_{1} \\ \mathrm{I} 3.8 \end{gathered}$ | Q | W | X | Z | No. of axial rings | No. of ribs |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  |  |  |  |  | Left | Right |
|  |  | - | I2.5 | - | - | - | - | - |
| In 36921 | 15.2 | $6 \cdot 0$ | 14.1 | $2 \cdot 6$ | 4.4 | 6+ | 3 | $2+$ |
| BM 59200 | II• 6 | $4 \cdot 8$ | 10.8 | $2 \cdot 3$ | $3 \cdot 8$ | 8+ | $3+$ | $3+$ |
| It. 2736 | c. $15 \cdot 0$ | - | - | c. $2 \cdot 5$ c. | $4 \cdot 1$ | 6+ | 4+ | 4+ |
| It. 2737 | - | - | - | $2 \cdot 7$ | $4 \cdot 3$ | $7+$ | $3+$ |  |
| OUM Bi79 | I6.0 | $5 \cdot 2$ | 12.9 | $2 \cdot 5$ | $4 \cdot 0$ | 9 | 3 | 2 |

All measurements in mm. For explanation of symbols see Text-fig. I. Measurements on BM 59200 were taken from a latex impression.

Type locality and horizon. The original label affixed to the holotype (figured Elles, 1940, pl. 3I, figs I, I $a$ as $T$. cf. foveolatus Angelin) states 'Trinucleus ornatus Sternb. Llandeilo Flags Gwernyfydd. Griffith Davies Coll.' The lithology is, however, completely different from that found at Gwern-yfed-fâch, Nr. Builth, but is very like that found at the small quarries 600 yds east of Upper Gilwern, and the presence of similar specimens at this locality suggests it to be the true locality for the holotype, and also paratypes In. 3692r, BM 59200. The evidence of the hand specimen is supported by thin sections taken from the holotype slab and Upper Gilwern material. Of the other paratypes, It. 2736 is from the small quarries 600 yds east of Upper Gilwern and OUM Bi79 is almost certainly from this locality also; It. 2737, It. 2738 are from the cliff section on the left bank of the Howey Brook half a mile east-south-east of Carregwiber.

Distribution. Apart from the two localities from which the type material is drawn, the species is also known from the exposures in the left bank of the track from Bwlch Ll̂̂yn to Hendy Bank, Ioo yds south-east of Bwlch Ilŵyn. All these localities are confined to the upper part of the Lower Llanvirn. At present the species is known only from the Builth inlier.

Description. Excluding the genal spines, the complete exoskeleton is oval in outline, but with the maximum cephalic width approximately equal to the total sagittal length.

The elliptical cephalon is about two and a half times as wide as long. The glabella is clavate in plan, strongly convex, extending slightly onto the fringe; three pairs of lateral glabellar furrows developed, the median pair marking the posterior of the prominent pseudofrontal lobe. In profile the glabella is strongly
convex anteriorly, levelling off medially and sloping gently down to the posterior. The anterior pair of lateral glabellar furrows, situated just anterior of the mid-point of the glabella, consist of small, weakly developed pit-like depressions in the side of the glabella. The median furrows are more strongly developed and are situated at about two-thirds the distance along the glabella from the anterior. The posterior furrows are well developed, slightly elongate sagittally and mark the front of the weakly developed occiput, near the rear of the glabella. Small crescentic alae are present, though poorly developed. A small median glabellar node is present on the external surface of the glabella situated approximately level with the median pair of lateral glabellar furrows. Medially the external surface of the glabella is covered with small closely spaced pits which may also be present on the sides of the glabella (Pl. 3, fig. 6).

The occipital ring is short (sag.), posteriorly convex, transversely arched and overlaps the anterior part of the axis of the first thoracic segment. The occipital furrow is wide and shallow with occipital pits being only weakly developed at the lateral extremities. No occipital spine is present.

Anteriorly the axial furrows are deep and narrow, becoming somewhat wider to the posterior. No anterior fossulae have been observed, but by analogy with other trinucleids it seems likely that they are developed.

The genal regions are transversely semi-oval, the outer margin being strongly convex, the inner margin strongly concave and the posterior margin more or less straight medially, curving forwards at the lateral extremities. The genae are moderately elevated with the outer parts sloping steeply down to the fringe. Externally they are, like the glabella, covered with small pits. Specimen It. 2738 (Pl. 3, fig. 6) shows, on the external surface, a single, unbranched genal caeca extending obliquely from the anterior lateral glabellar furrows to just outside the lateral pits. No eye tubercles or ridges are developed.

The posterior border furrow is moderately deep and narrow axially, becoming wider laterally and terminating in a shallow lateral pit. The posterior margin is straight medially, but is deflected forwards through about $40^{\circ}$ at the fulcral processes (Pl. 3, fig. 7).

Internally the lateral glabellar furrows and lateral pits form variably raised platforms. The small median glabellar node is not evident on the inside of the glabella.

The hypostoma is not known.
The fringe is about I .5 mm in width narrowing to about $\mathrm{I} \cdot 0 \mathrm{~mm}$ in front of the glabella. The upper lamella is gently convex, turning abruptly upwards at the edge to form a prominent rim. The marginal band is declined steeply downwards. Six arcs of pits are developed, the pits of the outer arc being larger than the remainder. The arcs present are probably $\mathrm{E}_{1}, \mathrm{I}_{1-5}$ but as the lower lamella is not known there is no way of being certain of this at present. The pits are arranged in shallow radial sulci separated by low, rounded ridges. The radial pattern is persistent, breaking down only at the genal angles. The holotype is the only specimen known showing the individual pits at all clearly; there being nineteen
pits in $E_{1}$ on the left half-fringe and about eighteen on the right half. The number of pits in the anteromedian rows cannot be determined but five I arcs are present by row 9 on either side of the fringe and continue to the genal angles. Irregularities in the pit distribution occur, the holotype showing two ridges fusing between row I3 and row 14 on the left half of the fringe, and between row 8 and row 9 on the right side (Pl. 3, fig. 7). The paratype OUM Bi79 (Pl. 3, fig. 4) possesses about 43 pits in the $E_{1}$ arc, of which about 2I are situated on the left half-fringe. The preservation of the inner portion of the fringe however does not allow determination of the number of arcs developed.

The facial suture is marginal, being near the bottom of the marginal band anteriorly and tending obliquely across it laterally to be just below the marginal rim at the posterolateral corners, whence it follows the posterior border of the fringe inwards towards the fulcral processes (Pl. 3, fig. 7). The genal spines are known on a single specimen, It. 2736 , in which the left spine extends behind the pygidium for about six mm.

The thorax is rectangular in shape, being about two and a half times wider than long. The six segments conform to the usual trinucleid pattern and require no further detailed account. The axial furrows are however better developed dorsally than in the type species.
The triangular pygidium is about three times as wide as long. The posterior margin is defined by a very small raised rim marking the upper limit of the steeply declined posterior border. The convex, clearly differentiated axis may have at least nine rings present, although they are only well developed anteriorly. Up to three faint ribs may be present on the pleural fields in addition to the anterior border (Pl. 3, fig. 4).

Biometrical data. Although relatively few specimens of this species are available, some bivariate analyses have been possible, as detailed below. No


Fig. 4. Reconstruction of the cephalon of Trimucleus abruptus sp, nov. in dorsal view.

$$
\text { c. } \times 5
$$

data apart from the few mentioned above in the description are available for the pit distribution or for the pygidial segmentation. All data refer to specimens from, or inferred to be from, the small quarries 600 yds east of Upper Gilwern, unless otherwise stated.

Table it

| x : y | $\overline{\mathrm{x}}$ | r. | $\overline{\text { y }}$ | var. y | r | $\mathrm{r}_{\mathrm{e}}$ | $\alpha$ | var. $\alpha$ | a | a |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| $\mathrm{I}_{1}$ : A | 14.15 | 1.9367 | 7.30 | - 6067 | - 0993 | -.993 | o8 | $0 \cdot 0078$ | 0.56 | -00209 |  |
| $\mathrm{K}: \mathrm{K}_{1}$ | $5 \cdot 18$ | -.1217 | o | 0.0280 | 959 | 0.960 | $1 \cdot 24$ | -.0305 | $0 \cdot 48$ | 0.00457 |  |
| W: Z | 10.74 | 5.3780 | $3 \cdot 58$ | 0.4920 | -.967 | -0.968 | 0.91 | 0.0173 | 0.30 | 0.00196 |  |
| $\mathrm{X}: \mathrm{Z}$ | $2 \cdot 20$ | 0.1500 | $3 \cdot 58$ | $0 \cdot 492$ | 0.985 | 0.985 | I•II | $0 \cdot \mathrm{I}$ | 1.81 | 0.03324 |  |

Bivariate statistics for Trinucleus abruptus sp. nov. from the small quarries 600 yds east of Upper Gilwern. All measurements in mm. For explanation of symbols see Text-fig. r.

## Table I2

|  | B | $\mathrm{B}_{1}$ | $\mathrm{~B}_{2}$ | $\mathrm{~B}_{3}$ |
| :--- | :---: | :---: | :---: | :---: |
| It. 2736 | $5 \cdot 8$ | $4 \cdot 6$ | $3 \cdot 5$ | $2 \cdot \mathrm{I}$ |
| In. 36920 | $6 \cdot 0$ | $5 \cdot 2$ | $4 \cdot 2$ | $3 \cdot 0$ |
| In. 3692I | $7 \cdot 0$ | $5 \cdot 7$ | $4 \cdot 5$ | $3 \cdot 4$ |
| BM 59200 | $6 \cdot 2$ | $5 \cdot 0$ | $4 \cdot \mathrm{I}$ | - |
| It. 8603 | $5 \cdot 5$ | $4 \cdot 5$ | $3 \cdot 6$ | $2 \cdot 5$ |
| BU 273 | $6 \cdot 4$ | $5 \cdot 4$ | 4.0 | - |

Data for the position of the lateral glabellar furrows for Trinucleus abruptus sp. nov. Specimen BU 273 from the cliff section in the Howey Brook. All measurements in mm. For explanation of symbols see Text-fig. i.

Table 13

|  | $\mathrm{R}_{1}$ | $Q$ | $\mathrm{R} / \mathrm{Q}$ |
| :--- | :---: | :---: | :--- |
| In. 3692 I | $\mathrm{I} \cdot 2$ | $6 \cdot \mathrm{O}$ | $2 \cdot 5$ |
| BM 59200 | $\mathrm{I} 2 \cdot 7$ | $4 \cdot 8$ | $2 \cdot 6$ |
| It. 8603 | $\mathrm{II} \cdot 6$ | $4 \cdot 8$ | $2 \cdot 4$ |
| It. 880 I | $9 \cdot 7$ | $4 \cdot \mathrm{I}$ | 2.4 |

Thoracic measurements for Trinucleus abruptus sp. nov. All measurements in mm. Measurements for It. 88 or taken from external mould. For explanation of symbols see Text-fig. $\boldsymbol{r}$.

Discussion. Although the position of the girder is not known, this species is placed in the genus Trinucleus Murchison on the assumption that the outer arc, with the larger pits, represents an $\mathrm{E}_{1}$ arc. This generic placing is supported by the general Trinucleus-like glabella and also by the close similarity between this species and Trinucleus acutofinalis Whittard, 1956.

Elles (1940: 425) compared this trilobite with Trinucleus foveolatus Angelin, 1854 . Apart from the difference in size noted by Elles, the present species differs in fringe shape, lack of eye tubercles, and also in the external surface 'ornament'. In addition the small median glabellar node is more pronounced on the external surface of $T$. abruptus, whereas in T. foveolatus it is apparently more prominent on the internal moulds. T. abruptus may be distinguished from the somewhat younger, but closely related $T$. acutofinalis by the presence of at least six arcs of pits, and also by the lateral continuation of the sharp upper external rim of the upper lamella. The pygidia of the two species may be separated on the higher number of axial rings and pleural ribs in T. acutofinalis. T. fimbriatus is readily distinguished by the presence of genal prolongations to the fringe, and a relatively wider pygidium with more ribs. Trinucleus bronni Sars and Boeck in Boeck, 1838 is distinguished by having only two to four arcs of pits developed and also in possessing lateral eye tubercles.

Although very little information is available, it would appear from the holotype that the same kind of irregularities in the pit distribution as found in $T$. fimbriatus are also present in T. abruptus.

A single lower lamella, here described as Anebolithus sp. (p. I39, Pl. 4, figs. 3, 5) having no E arcs developed, is known from the type locality of $T$. abruptus, but it differs in outline, particularly at the genal angles. However until such time as a lower lamella is discovered in place in T. abruptus there remains the possibility that this species may be better placed in Anebolithus Hughes and Wright, 1970.

## Trinucleus cf. acutofinalis Whittard

## (Pl. 3, fig. 5; Pl. 4, figs 4, 7, 8)

Figured material. It. 2739 (Pl. 3, fig. 5) Internal and external moulds of anterior thoracic segment. It. 274I (Pl. 4, fig. 4) Internal mould of pygidium and part of thorax. It. 2742 (Pl. 4, fig. 8) Internal and external moulds of damaged cranidium. It. 2743 (Pl. 4, fig. 7) Internal and external moulds of nearly complete specimen.

Locality and horizon. All the figured specimens are from the ashy mudstones and sandstones at the top of the Cwm-Amliw Ash (Didymograptus murchisoni Zone) exposed in the stream section about 200 yds south-west of Wern Ddu Barn. Specimens It. 2739-2742 being from the left bank, and specimen It. 2743 from the right bank. These are the only two localities from which the species is known.

Description. The cephalon is slightly over two and a half times as wide as long. Anteriorly the margin is only slightly curved, but becomes more strongly so laterally. The posterior margin is straight axially but is deflected forwards at the fulcrum. The glabella is typically trinucleinid with a swollen anterior portion; details of the lateral glabellar furrows are not known. No indication of any median glabellar node is preserved. The external surface of the genal regions is covered
with numerous small pits (Pl. 4, fig. 7). A single genal caeca is developed commencing opposite the mid-point of the glabella and directed obliquely to the genal angle. No eye tubercles or ridges appear to be present. The fringe is narrow and has a prominent marginal rim anteriorly and laterally. Details of the pit distribution are poorly known but it seems probable that four arcs of pits are developed, the inner one or two arcs being absent anteromedially due to the slight encroachment of the glabella onto the fringe. The pits are sunk into radial sulci, there being between seventeen and twenty rows on each half-fringe. Posterolaterally, interradial rows with pits of the inner two arcs may be developed (Pl. 4, fig. 8). The position of the girder is not indicated on the upper lamella, though it is possible that the outer arc is external to the girder due to the slightly larger size of the pits.

The thorax appears to conform to the usual trinucleid pattern. As in T. acutofinalis and T. abruptus sp. nov., the pleural termination of the anterior thoracic segment is markedly oblique (Pl. 3, fig. 5).

The triangular pygidium is nearly three times as wide as long. At least four axial rings and two pleural ribs are developed. Posteriorly the preservation deteriorates, and it is impossible to ascertain if these are the total number of rings and ribs developed.

Discussion. This species is important, for apart from a few incomplete specimens occurring near the base of the Lower Didymograptus murchisoni shales, this is the only trinucleid known from the Upper Llanvirn of Builth. Obvious similarities exist between this form and T. acutofinalis Whittard from the Betton beds of the Shelve region (Upper part of D. murchisoni Zone) with regard to the general outline and fringe details. The marginal rim however, does not diminish laterally and the pygidium has fewer axial rings and pleural ribs than T. acutofinalis. In these latter features $T$. cf. acutofinalis is more like T. abruptus from the upper part of the Lower Llanvirn. However, owing to the probable development of only three I arcs it is thought that these Builth specimens are most closely related to T. acutofinalis.

The attitude of the exoskeleton of specimen It. 2743 (Pl. 4, fig. 7) is of interest as the thorax and pygidium are sagittally concave dorsally in a manner akin to, though more pronounced than, the specimen of Tretaspis seticornis (Hisinger, 1840) figured by Størmer (1930, fig. 47).

Genus ANEBOLITHUS Hughes and Wright, 1970
Diagnosis. See page izo.
Type species. Incaia simplicior Whittard, 1966.
Distribution. Lower Arenig and Lower Llanvirn of the Welsh Borderland.
Discussion. The genus has recently been discussed together with Incaia in Hughes and Wright, 1970, and no further discussion is necessary.

## Anebolithus sp.

(Pl. 4, figs 3, 5)
Figured specimen. It. 2744 Internal and external moulds of lower lamella.
Horizon and locality. Uppermost part of the Lower Llanvirn (Subzone D. speciosus) from the small quarries 600 yds east of Upper Gilwern.

Description. A single specimen is known of a lower lamella apparently having no pits developed external to the girder. It is 14 mm in width at the posterolateral extremities; the estimated cephalic length being about 6.5 mm . The seemingly smooth girder is well developed and nearly semicircular in outline. Traces of two or three arcs of pits internal of the girder are visible with radially arranged pits on most of the convex genal roll. Long outwardly curved genal spines are present extending about 12.5 mm from the posterolateral extremities of the girder, their maximum separation being 16.5 mm which occurs at approximately one-third of their total length as measured from the anterior.

Discussion. Unless the absence of pits external to the girder is due to imperfect preservation it seems that this single specimen is best placed in Anebolithus Hughes and Wright, 1970. Its outline, particularly near the genal angles appears to preclude it from being the lower lamella of $T$. abruptus. With only the lower lamella, no adequate comparison can be made with the only other known species of the genus. However it is noteworthy that the Builth specimen is larger and is more smoothly rounded anteriorly than is the case in $A$. simplicior (Whittard, 1966) from the Lower Arenig at Shelve.

## Genus BERGAMIA Whittard, 1955

1966 Cochliovrhoe Whittard.
Diagnosis. See page izo.
Type species. Bergamia rhodesi Whittard, 1955.
Distribution. The genus is known from the British Isles where it is recorded from beds ranging from the Arenig to basal Caradoc, and from the Llandeilo (Dobrotivá Formation) of Czechoslovakia. The genus may also be present in the Upper Llanvirn (4a $\alpha$ ) of Norway (Bruton, pers. comm.).

Discussion. In erecting Bergamia in 1955 Whittard defined his genus as typically bearing $E_{1}, E_{2}$ and $I_{1}$ arcs, fully developed. In 1966 , following the discovery of forms apparently lacking between three and five pits of the $\mathrm{E}_{2}$ arc anteromedially, he erected the genus Cochliorrhoe to accommodate forms with $\mathrm{E}_{2}$ only partially developed. However, the type species of Bergamia, B. rhodesi Whittard, has an $\mathrm{E}_{2}$ pit lacking posterolaterally and might therefore be placed within Cochliorrhoe if his diagnosis were strictly followed. It is now known that Bergamia whittardi sp. nov. (see p. 146), in common with other trinucleids shows some variation in the total number of pits developed in each arc and in particular in the $\mathrm{E}_{2}$ arc which is only well developed anterolaterally. In both Bergamia and Cochliorrhoe the $\mathrm{E}_{2}$ arc may first appear as twin-pits within the $\mathrm{E}_{1}$ arc, and from the fringe formulae listed
by Whittard (1966: 279-280) it appears that the essential difference between his two genera was that in Cochliorrhoe two separate arcs cannot be distinguished, possessing either twinned or distinctly separate pits, until between rows three and five. Although it has been the practice in recent years to base the trinucleid genera on the particular arcs developed, it is thought that the partial development of the $\mathrm{E}_{2}$ arc does not warrant generic status and it is proposed to consider Cochliorrhoe Whittard, ig66 as a junior synonym of Bergamia Whittard, 1955.

Bergamia is closely related to Lordshillia Whittard, 1966, Stapeleyella Whittard, 1955 and Anebolithus Hughes and Wright, 1970, but it may be readily distinguished by the presence of the $\mathrm{E}_{2}$ arc partially or fully developed. Bergamia also shows some similarities to Tretaspis M'Coy, 1849, but differs in that it has no lists developed between the I arcs of the upper lamella, or eye ridges or tubercles on the genal regions as are typical of Tretaspis.

The occurrence of Bergamia prima (Elles) and Bergamia whittardi sp. nov. is of interest as it is the first record of the genus from the Llandeilo of Britain, it being known previously only from the Llandeilo (Dobrotivá Formation) of Czechoslovakia (Přibyl and Vaněk, 1969). (It is considered by the present author that 'Tretaspis' praecedens Klouček, igI6 was correctly placed in the genus Bergamia by Prribyl and Vaněk.) Other previous British occurrences are from the Arenig of South Wales and Shropshire, Lower Llanvirn of Anglesey and from the basal Caradoc of south-east Ireland.

## Bergamia prima (Elles)

(Pl. 4, figs I, 2, 6; Pl. 5, figs I-6; Pl. 6, figs $1-6,8$; Text-fig. 5)
1940 Trinucleus fimbriatus mut. primus Elles: pars, 4 IO-412, $4^{21}$, 424, pl. 30, figs 1-3 non 4, 5 which are B. whittardi.
Diagnosis. Bergamia with about twenty to twenty-three pits developed in $\mathrm{E}_{1}$ and $E_{2}$ arcs on each half-fringe ; pits of $E$ arcs very close together particularly anterolaterally. Pygidium short, with five or six axial rings and three or four pleural ribs.

Type material. Holotype. BU 257 (Pl. 4, fig. 6; Pl. 5, figs I, 2) (Chamberlain Collection) Internal and external moulds of nearly complete specimen.

Paratypes. BU 258 (Chamberlain Collection) Internal mould of incomplete specimen. BU 259 (Chamberlain Collection) External mould of cephalon.

Dimensions.

|  | A | B | $\mathrm{B}_{1}$ | $\mathrm{~B}_{2}$ | $\mathrm{~B}_{3}$ | $\mathrm{~B}_{4}$ | $\mathrm{I}_{1}$ | K | $\mathrm{~K}_{1}$ |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Holotype | - | $c .5 \cdot 4$ | $c .4 \cdot 4$ | $c .3 \cdot 3$ | $c .2 \cdot \mathrm{I}$ | $c .2 \cdot \mathrm{I}$ | $c . \mathrm{I} 2 \cdot 2$ | $4 \cdot 4$ | $2 \cdot 2$ |  |
| BU 258 | $c .7 \cdot 0$ | - | - | - | - | - | - | - | - |  |
| BU 259 | - | $c .6 \cdot 6$ | - | - | - | - | $c .12 \cdot 5$ | $c .5 \cdot 0$ | - |  |
|  |  |  |  |  |  |  |  | No. of | No. of ribs |  |
|  | $\mathrm{R}_{1}$ | Q | $\mathrm{Q}_{1}$ | W | X | Z | axial rings | Left | Right |  |
| Holotype | $\mathrm{I} 2 \cdot 8$ | $5 \cdot 0$ | $\mathrm{I} \cdot \mathrm{O}$ | $9 \cdot 8$ | $2 \cdot 3$ | $2 \cdot 5$ | 5 | 4 | 4 |  |

All measurements in mm. For explanation of symbols see Text-fig. i.

Type locality and horizon. The type specimens are all from the shales assigned to the Zone of $G$. teretiusculus exposed in the old quarry 350 yds west of Maesgwynne.

Other figured material. It. 2745 (Pl. 4, figs I, 2) ; It. 2746 (Pl. 5, figs 3, 4); It. 2747 (Pl. 6, figs 2, 3) ; It. 2748 (Pl. 6, fig. 5) ; It. 2749 (Pl. 5, fig. 6) ; It. 2750 (Pl. 6 figs I, 4) ; It. 275 I (Pl. 6, fig. 6) ; It. 2752 (Pl. 6, fig. 8) ; It. 2753 (Pl. 5, fig. 5).

Distribution. The species is known only from the Builth region, being recorded with certainty only at the type locality and the stream section 15 yds south-west of the type locality.

Description. Excluding the genal spines, complete specimens are approximately circular in outline.

The semicircular cephalon varies between two and two and a half times as wide as long, excluding the steeply declined fringe. The strongly convex, clavate glabella is elevated well above the genae, overhanging and obscuring the fringe anteriorly. The swollen pseudofrontal lobe is just over one-half of the glabellar length and bears a median node, generally discernible on both internal and external moulds, situated somewhat variably, but generally immediately behind the anterior of the three pairs of lateral glabellar furrows. These furrows occur at about two-fifths of the distance along the glabella from the anterior, and consist of small pit-like depressions in the side of the glabella. The median furrows, marking the posterior of the pseudofrontal lobe, are elongate ( $t r$.) pits which extend about half the distance to the sagittal line. The posterior furrows are also elongate (tr.) pit-like structures directed anteromedially. Both the median and posterior pairs of lateral glabellar furrows are situated well inside the axial furrows and alae are developed ( Pl .5 , figs. 5, 6). A similar depression to that described in Trinucleus fimbriatus occurs laterally and slightly posteriorly to the posterior pair of lateral glabellar furrows (Pl. 5, fig. 2). The occiput is generally slightly less than half as wide as the pseudofrontal lobe. A coarse reticulate pattern is developed over the entire external surface of the glabella.

The occipital ring is very short (sag.), transversely convex and has no occipital spine. The occipital furrow is shallow medially deepening laterally forming elongate ( $t r$.) occipital pits.

Anteriorly the axial furrows are deep and narrow. Posteriorly they converge slightly and become wider and shallower; the alae being situated between the furrows and the glabella. Anterior fossulae are usually poorly preserved.

The genal regions are quadrant-shaped, moderately tumid, with the outer margin declined steeply, and possess a reticulate pattern which becomes less pronounced peripherally on the steep outer margins and posteromedian portions of the genae. No eye ridges or tubercles occur. The posterior border furrow is straight, wide and rather shallow; lateral pits well developed though rarely well preserved (Pl. 6, fig. 4).

The internal surface of the glabella and genae is smooth. The lateral glabellar furrows form raised platforms internally, and small apodemes, corresponding to the anterior fossulae, are present.

The hypostoma is not known.

Although commonly distorted, the fringe probably possessed a steep, nearly vertical genal roll, which flattened out towards the brim. The narrow fringe widens somewhat at the genal angles. Owing to poor preservation, there is very little information concerning the distribution of pits on the fringe. All pits are small and appear to be of approximately equal size. They are arranged in shallow radial sulci separated by low rounded ridges (Pl. 5, fig. 6). The $E_{1}$ and $E_{2}$ arcs are continuous medially and contain between twenty and twenty-three pits on each halffringe; at the posterolateral extremity only the $\mathrm{E}_{1}$ arc is developed. The number of arcs present internal to the girder is uncertain, but probably does not exceed two anteromedially, with up to four present posterolaterally (Pl. 5, fig. 4; Pl. 6, figs I, 2).

The lower lamella is nearly flat medially, but laterally the girder forms a strong ridge separating an almost flat outer part from a steeply inclined inner region. The $\mathrm{E}_{1}$ and $\mathrm{E}_{2}$ are sunken into short sulci and are very close together; at the anterolateral corners they merge into little more than a single arc of twin pits (Pl. 4, fig. I; Pl. 5, fig. 3; Pl. 6, fig. 3). The girder is apparently smooth and well formed except anteromedially. Posterolaterally it merges with the base of the genal spine. Medially some irregularities may occur with pits of the $\mathrm{E}_{2}$ arc being absent (Pl. 6, figs 2, 3).

The genal spines are approximately straight, diverging slightly to the rear and with a low dorsal keel ; they extend well behind the pygidium (Pl. 4, fig. 6). The entire course of the facial suture has not been traced, but laterally it is marginal, situated high on the marginal band, and becomes dorsal at the genal angle.

The thorax consists of six segments and conforms to the general trinucleid type. It is not more than about two and a half times as wide as long, and narrows slightly to the rear. The distal extremities of the pleurae are deflected posteriorly and ventrally, the amount of deflection becoming progressively greater posteriorly. A strong pleural ridge divides the pleurae into a small posterior and a larger anterior band. A small median node is present on the anterior portion of the axis of each segment (Pl. 4, fig. 6).


Fig. 5. Reconstruction of the cephalon of Bergamia prima (Elles) in dorsal view. c.

The triangular pygidium is slightly less than four times as wide as long. Excluding the articulating half ring, the anterior margin is straight except for the posteriorly directed lateral extremities. The posterior and lateral margins are marked by a low ridge at the upper limits of the steeply declined border region, with closely spaced terrace lines developed on the external surface. The axis is convex, clearly differentiated and segmented, with between three and six axial rings plus a small terminal piece. The axis continues posteriorly as a convex protuberance on the border region (Pl. 5, fig. 5). Anteriorly the axis occupies about one-fifth of the width of the pygidium, tapering posteriorly to about half this width. As is usual in the trinucleids the axial furrows are slightly more prominent on internal than external moulds. The pleural fields are flat and each has an anterior border, usually three or four ribs (rarely two), and a small triangular terminal area. The furrows separating the ribs are straight, sub-parallel and directed slightly to the posterior.

The species exhibits discoidal enrollment as is normal in the trinucleids ( Pl .6 , fig. 8).

Ontogeny. Of the two small specimens known from the stream section 15 yds south-west of the type locality, the larger has a maximum genal width of 4.6 mm and is assocated with four slightly disarticulated thoracic segments and a pygidium, and may thus represent a meraspid degree four. Apart from their size, the specimens are similar to larger individuals, except that the głabella and genal regions are more highly convex (Pl. 6, fig. 5).

Dimensions.

|  | A | $\mathrm{A}_{1}$ | B | $\mathrm{~B}_{1}$ | $\mathrm{~B}_{2}$ | $\mathrm{~B}_{3}$ | $\mathrm{~B}_{4}$ | $\mathrm{I}_{1}$ | K | $\mathrm{~K}_{1}$ |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| It. 2748 | 2.6 | 2.4 | 2.2 | I .8 | I .4 | - | $\mathrm{II} \cdot \mathrm{I}$ | 4.6 | I .4 | 0.7 |

All measurements in mm . For explanation of symbols see Text-fig. I.
Biometrical data. Various analyses were undertaken on the major features of the dorsal exoskeleton. Since data for the type locality sample is rather scant, data is also given for the total sample from the inlier.

| $\begin{gathered} x: y \\ p \end{gathered}$ | $\overline{\bar{x}}$ $5 \cdot \mathrm{I}$ | var. x 0.9730 | $\bar{y}$ | $\begin{aligned} & \text { var. y } \\ & 0.5850 \end{aligned}$ |  | $\mathrm{r}_{\mathrm{e}}$ | 0.97 | var. $\alpha$ o.OI 58 | $\begin{gathered} \mathrm{a} \\ 0.78 \end{gathered}$ | var. a | 5 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| $\mathrm{I}_{1}: \mathrm{B}$ | $9 \cdot 38$ | $7 \cdot 4444$ | 4.17 | 1.5625 | 0.976 | 0.977 | 1.03 | 0.0069 | 0.46 | 0.00141 | 9 |
| A: B | $4 \cdot 70$ | $2 \cdot 0850$ | $4 \cdot 26$ | $2 \cdot 1630$ | 0.997 | 0.998 | 1-12 | 0.0020 |  | - | 5 |
| $\mathrm{B}: \mathrm{B}_{1}$ | $4 \cdot 29$ | 1-8958 | 3.33 | 1.1106 | 0.984 | 0.985 | - 99 | 0.0026 | $0 \cdot 77$ | 0.00164 | 13 |
| $\mathrm{B}: \mathrm{B}_{2}$ | $4 \cdot 49$ | 1.7961 | $2 \cdot 84$ | -0.7334 | 0.985 | 0.986 | I.OI | 0.0024 | 0. 64 | 0.00102 | 14 |
| $\mathrm{B}: \mathrm{B}_{3}$ | $3 \cdot 66$ | 1.4330 | $1 \cdot 50$ | - 1650 | 0.997 | 0.998 | 0.83 | 0.0008 | - 34 | 0.0002 | 5 |
| B : K | $4 \cdot 23$ | 1.4450 | $3 \cdot 35$ | I 1507 | 0.978 | 0.979 | 1. 12 | 0.0037 | - | - | 16 |
| $\mathrm{K}: \mathrm{K}_{1}$ | 3.42 | 1.4976 | $1 \cdot 50$ | 0. 2560 | 0.983 | 0.984 | 0.95 | 0.0031 | 0.41 | .00062 | II |
| W: X | $6 \cdot 40$ | 3.9950 | 1.24 | 0. 2480 | 0.974 | - 0.977 | I. 27 | 0.0238 | 0.25 | 0.00104 | 5 |
| X: Z | 1.46 | 0.1776 | $1 \cdot 79$ | $0 \cdot 1774$ | 0.824 | 0.830 | 0.82 | 0.0191 | 1.0 | 0.02909 | 13 |

Bivariate statistics for Bergamia prima (Elles). Upper part of table for the type locality sample; lower part for the total sample from the inlier. All measurements in mm . For explanation of symbols see Text-fig. I.

## Table 15

|  | B | $\mathrm{B}_{1}$ | $\mathrm{~B}_{2}$ |
| :--- | :---: | :--- | :--- |
| It. 2750 | $5 \cdot 7$ | 4.3 | 3.6 |
| It. 2753 | $5 \cdot 5$ | - | 3.2 |
| It. 8805 | $5 \cdot 0$ | - | $3 \cdot 2$ |
| It. 8803 | $6 \cdot 2$ | 4.7 | 3.8 |
| It. 8804 | $6 \cdot 0$ | 4.9 | $3 \cdot 9$ |

Data for the position of the lateral glabellar furrows for Bergamia prima (Elles) from the type locality. Data are insufficient to give meaningful bivariate statistics. All measurements in mm . Measurements for It. 8805 taken from external mould. For explanations of symbols see Text-fig. 1.

Table 16

|  | $\mathrm{R}_{1}$ | $Q$ |
| :--- | :---: | :---: |
| BU 257 | $\mathrm{I} 2 \cdot 8$ | $5 \cdot 0$ |
| It. 2753 | $\mathrm{II} \cdot 3$ | $5 \cdot \mathrm{I}$ |
| NMW 68.376.GI89 | $7 \cdot 0$ | $3 \cdot \mathrm{I}$ |
| NMW 68.376.GIgo | $9 \cdot 8$ | $4 \cdot 0$ |

Thoracic measurements for Bergamia prima (Elles). First two specimens from the type locality. All measurements in mm . For explanation of symbols see Text-fig. I.

Table I7

|  | W | X | Z |
| :--- | :---: | :---: | :---: |
| BU 257 | $9 \cdot 8$ | $2 \cdot 3$ | $2 \cdot 5$ |
| It. 2753 | $8 \cdot 5$ | $\mathrm{I} \cdot 7$ | $2 \cdot 3$ |
| NMW 68.376.GIgI | - | $\mathrm{I} \cdot 9$ | $2 \cdot 2$ |
| It. 8802 | - | $\mathrm{I} \cdot \mathrm{I}$ | $\mathrm{I} \cdot 5$ |
| NMW 68.376.GIg2 | - | $\mathrm{I} \cdot 9$ | $2 \cdot 4$ |

Pygidial measurements for Bergamia prima (Elles), from the type locality. All measurements in mm . For explanation of symbols see Text-fig. $\mathbf{I}$.

## Table 18

| Number of axial rings | 3 | 4 | 5 | 6 |
| :---: | ---: | ---: | ---: | ---: |
| Number of specimens | - | - | 3 | I |
| $n=4$ |  |  |  |  |
| Number of axial rings | 3 | 4 | 5 | 6 |
| Number of specimens | I | 7 | 12 | I |
| $n=21$ |  |  |  |  |

Frequency distributions for the number of pygidial axial rings developed in Bergamia prima (Elles). Upper part of table for the type locality sample; lower part for the total sample from the inlier.

Table I9

| Number of pleural ribs | 2 | 3 | 4 |
| :--- | ---: | ---: | ---: |
| of specimens |  | 6 | 2 |
| $n=8$ |  |  |  |
| Number of pleural ribs | 2 | 3 | 4 |
| Number of specimens | I | 13 | 14 |

Frequency distributions for the number of pygidial pleural ribs developed in Bergamia prima (Elles). Upper part of table for the type locality sample; lower part for the total sample from the inlier.

Discussion. Owing to the poor preservation of the fringe on much of the material available, Elles (1940: 424) erroneously believed this species to occur at Pencerrig Quarry, and to be conspecific with a form from Pencerrig Lake quarry which she considered as a mutuational form of Trinucleus fimbriatus Murchison, 1839. The presence of the two arcs of pits external to the girder clearly separates this species from T. fimbriatus and indicates its relationship to the genus Bergamia Whittard, 1955. The superficially similar form occurring at Pen-cerig Lake quarry is here referred to Bergamia whittardi sp. nov., and may be distinguished from Bergamia prima by the $\mathrm{E}_{2}$ arc being present only anteriorly.

Bergamia rhodesi Whittard, 1955 is similar to B. prima, but with apparently slightly fewer pits in each arc. However, the data at present available are insufficient to determine the amount of variation of the number of pits in each arc for either of these two forms. Subsequent collecting may well show them to be synonymous, in which case B. prima (Elles) would take priority. B. prima is easily distinguished from $B$. praecedens, (Klouček) by the smaller number of pits along the posterior margin of the fringe, the closeness of the $\mathrm{E}_{1}$ and $\mathrm{E}_{2}$ arcs and the differing surface sculpture on the glabella. B. prima is distinguished from B. inquilium (Whittard, Ig66) and B. matura Whittard, Ig66, which are thought to represent but a single species, by its greater number of pits in the E arcs and the median development of the $\mathrm{I}_{2}$ arc. 'Trinucleus' gibbsi Murchison, 1859, 'Trinucleus' sedgwicki Salter, 1866 and 'Trimucleus' etheridgei Hicks, 1875 were provisionally placed by Whittard in Bergamia. B. gibbsi may be distinguished by its apparent lack of pits internal to the girder lateral to row 8. B.? sedgwicki appears to be similar to $B$. prima in general shape and in the presence laterally of three arcs internal to the girder, but differs in having fewer pits in the $\mathrm{E}_{1}$ and $\mathrm{I}_{1}$ arcs. B.? etheridgei is here considered as a nomen dubium (see Whittard, 1955:35), on account of the poor preservation of the type specimens. Preliminary studies on 'Trinucleus' hibernicus Reed, 1895 from the Tramore Limestone Series support Whittard's (1955:31) view that the species is best placed in Bergamia, as $\mathrm{E}_{2}$ arc is fully developed, excepting for two or three pits at the posterolateral extremities of the arc, while one arc occurs internal to the girder. It is easily distinguished from B. prima by this single I arc, further, the separation of the two E arcs is greater in B. hibernicus. The specimens referred to Bergamia (?) sp. by Bates (1968: 184-185, pl. 13, figs 3, 4, 9, r3) from the

Lower Llanvirn of Anglesey are clearly referable to this genus though insufficient detail is known to allow proper comparisons with other known species.

## Bergamia whittardi sp. nov.

(Pl. 6, fig. 7; Pl. 7, figs I-12 ; Pl. 8, figs I-9, II ; Pl. 9, figs 1, 2; Text-figs 6, 7)
${ }_{1851}$ Tretaspis fimbriatus (Murchison); Sedgwick and M'Coy: pars, 146, pl. IE, figs 16, 16a. 1914 Trinucleus fimbriatus Murchison; Reed: pars, 350-352, 354, pl. 28, figs I, 3, non fig. 2. 1940 Trinucleus fimbriatus mut. primus Elles: pars, 410-412, 421, 424, pl. 30, figs 4, 5 .

Diagnosis. Bergamia with up to fourteen pits present anteromedially in $\mathrm{E}_{2}$ arc (full-fringe), $\mathrm{E}_{1}$ arc fully developed with about twenty-six to thirty pits (half-fringe); $\mathrm{I}_{1-5}$ arcs developed laterally.

Type material. Holotype. BU 260a (Chamberlain Collection) (Pl. 7, fig. 6) (figured as Trinucleus fimbriatus mut. primus by Elles, 1940, pl. 30, fig. 5) Mould of dorsal surface of incomplete lower lamella.

Paratypes. It. 2754 (Pl. 7, fig. 12) Internal mould of nearly complete specimen. It. 2755 (Pl. 8, fig. 3) External mould of nearly complete specimen. It. 2756 (Pl. 7, fig. 7) Fragment of mould of dorsal surface of lower lamella. It. 2757 (Pl. 8, fig. 7) Internal mould of cephalon. It. 2758 (Pl. 7, fig. io) Internal mould of nearly complete specimen. It. 2759 (Pl. 7, fig. 3) Fragment of mould of dorsal surface of lower lamella. It. 2760 (Pl. 8, fig. I) Internal mould of nearly complete specimen. Wattison Collection Hr4 (Pl. 8, fig. 9) Internal mould of damaged cephalon.

Dimensions.

| It. 2754 |  | A |  | $5 \cdot 7$ |  | $\begin{array}{r} \mathrm{B}_{2} \\ 3.8 \end{array}$ | $\begin{gathered} \mathrm{B}_{3} \\ 2.6 \end{gathered}$ | $\mathrm{B}_{4}$ |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | $45$ |  |  |  |  |  |  |
| It. 2755 |  |  | - | $2 \cdot 6$ | $2 \cdot 0$ | 1.6 | I. 2 | - | I.o | - |
| It. 2758 |  | - | - | $2 \cdot 3$ | 1.9 | I. 4 | 0.9 | - | 57 |
| Wattison Coll. Hi4 |  | c. $8 \cdot 0$ | - | - | $5 \cdot 1$ | 4.0 | $2 \cdot 9$ | 3.00 | 15.0 |
|  |  |  |  |  |  | No. of axial rings |  | No. of ribs |  |
|  | $\mathrm{R}_{1}$ | Q | W | Z | W |  |  | Left | Righ |
| It. 2755 | $4 \cdot 5$ | I.9 | 3.6 | 0.7 | 0.8 | $3+$ |  | 3 | , |
| It. 2757 |  | - | $10 \cdot 3$ | $3 \cdot 1$ | 2.7 | 6 |  | 4 | 4 |
| It. 2758 c. | c. 5.7 | 2.5 | 47 | 0.8 | I-2 | $4+$ |  | 3 | 3 |

All measurements in mm . For explanation of symbols see Text-fig. I.
Fringe data for holotype. Left half-fringe: $E_{1} 1-c .27 ; \mathrm{E}_{2} \mathrm{I}-c .7 ; \mathrm{I}_{1} \mathrm{I}-c .2 \mathbf{I} ; \mathrm{I}_{2} \mathrm{I}-c$. 19; $I_{3}$ I-c. 19 ; $I_{4}$ II-c. $19 ; I_{5}$ I7-c. 19. Auxiliary pit: xvi, xvii, xviii present in $I_{3-5}$. Number of radial rows $c$. 19 .

Type locality and horizon. The holotype and all the paratypes are from the small quarry at the south-western end of Pen-cerig Lake in shales of the uppermost

Llandeilo, with the exception of paratype It. 2760 which is from shales of Llandeilo age from the stream section 120 yds south-east of Tre coed.

Other figured material. It. 276 (Pl. 7, fig. 9) ; It. 2762 (Pl. 7, fig. 1) ; It. 2763 (Pl. 8, fig. II) ; It. 2765 (Pl. 9, fig. I); It. 2766 (Pl. 7, fig. 8) ; It. 2767 (Pl. 9, fig. 2); It. 2768 (Pl. 8, fig. 4) ; It. 2769 (Pl. 8, fig. 8) ; It. 2770 (Pl. 8, fig. 5) ; It. 277 (Pl. 7, fig. 5) ; It. 2772 (Pl. 7, fig. 2) ; It. 2773 (Pl. 6, fig. 7) ; It. 2774 (Pl. 8, fig. 6); It. 2775 (Pl. 8, fig. 2) ; It. 2776 (Pl. 7, fig. 4); It. 2778 (Pl. 7, fig. II).

Distribution. The species has only been recorded from the Llandeilo of the Builth region. It is extremely abundant in the Pen-cerig Lake quarry and is also known from the Dulas Brook as well as the other locality from which the type material is drawn.

Description. Excluding the genal spines, complete specimens are generally subcircular to oval in outline (Pl. 7, fig. 10; Pl. 8, fig. 2).

The cephalon is semicircular and, excluding the fringe, varies between two, and two and a half times as wide as long. The clavate glabella, its furrows and the occipital ring are similar to those of Bergamia prima. The median glabellar node is typically not well developed on internal moulds, while axial furrows and alae are again very similar in the two species.

The genal regions are quadrant-shaped, less tumid than in B. prima and have a strong reticulate pattern which is most coarsely developed along a diagonal band from the genal angles to the antero-median corner of each genae. No eye ridges or tubercles are present. The posterior border furrows are wide, shallow and more or less straight, terminating in clearly developed lateral pits. Rarely, traces of the


Fig. 6. Reconstruction of the cephalon of Bergamia whittardi sp. nov. in dorsal view. c. $\times 1$.
reticulate pattern are present in internal moulds (Pl. 8, fig. 9). Internal platforms reflecting the lateral glabellar furrows are present as in B. prima.

The hypostoma is not known.
The preservation of the fringe varies considerably. In the majority of specimens the fringe is fairly flat, commonly showing signs of cracking around its inner margin (Pl. 8, fig. 9). In a few specimens, however, the genal roll is steeply inclined as in B. prima. Although much of the flattening of the fringe may be attributed to preservation in shale, it is considered that the initial inclination of the fringe of B. whittardi may not have been so great as in B. prima. The pits are arranged in shallow radial sulci which are separated by low rounded ridges. The pits of the $E_{1}$ and $I_{1}$ arcs are larger than the rest, which are small and subequal in size. Dorsally the pits of the anteromedially developed $E_{2}$ arc are very close to those of the $E_{1}$ arc and give the impression of twin-pits; ventrally the pits, although closely spaced, are separated and represent two distinct arcs (Pl. 7, figs 3, 6, 7).

Insufficient data are available to allow a full statistical description of the pit distribution on the fringe, but the following observations may be made. The number of pits in the $E_{1}$ and $I_{1}$ arcs varies between about twenty-four and thirty. The development of the $\mathrm{E}_{2}$ arc anteromedially appears to vary, but at least seven pits are present on the half-fringe of the holotype. Specimen It. 2754 suggests, however, that the pits of the $E_{2}$ arc are not always present in all the anteromedian rows. Only a single specimen, It. 2754, shows the arc internal to the girder at all clearly (Pl. 7, fig. I2). On the left half-fringe of this specimen arcs $I_{1}$ and $I_{2}$ are present medially with $I_{3}$ appearing at row four, $I_{4}$ at row nine and $I_{5}$ at row twelve. The genal flanges are large and consist of an outer fimbriate zone incorporating the pits of the $E_{1}, I_{1}$ and $I_{2}$ arcs, and an inner fimbriate zone with four or five pits in each row developed along the margin of the genae and along the posterior border. Up to about twelve rows of pits may be present in this inner zone. The central triangular area between the two fimbriate zones has its pits irregularly positioned (Pl. 7, fig. 12). The genal flange has up to seven or eight $\mathrm{E}_{1}$ pits on its posterior extension from the cephalon.

The facial suture is marginal medially where it is situated very high on the marginal band becoming dorsal at the genal angles. The girder merges posterolaterally with the base of the genal spines. Only the anterior portions of the genal spines are known and are gently curved in a smooth arc continuous with the lateral cephalic margins.

The thorax is typically trinucleid and is very similar to that of B. prima. The extremities of the pleurae are however slightly less strongly deflected posteriorly (Pl. 7, fig. r).

The triangular pygidium is about four times as wide as long, with the anterolateral corners deflected slightly posteriorly as noted in the thoracic segments. The number of axial rings ranges from five to seven, with two to four pleural ribs. In all other features the pygidium is very similar to that of $B$. prima.

Ontogeny. The only certain meraspis is of degree four and has the posterior margin of the fringe directed anterolaterally from the genal angle in a similar manner
to that found in the meraspis of Trimucleus fimbriatus. On the other hand, the smallest certain holaspis has well-developed genal flanges extending posterior to the cephalon (Pl. 7, fig. II ; Pl. 9, fig. I). It seems reasonable to assume that other small isolated cephala with the posterior border of the fringe directed either anterolaterally or transversely are also late meraspides. The degree four meraspis is about 4 mm in length and is very like the holaspid form apart from the number of segments and the anterolaterally directed posterior margin of the fringe. The genae rise fairly steeply from the axial furrows, leaving the posterior part of the axial furrows and the alae rather sunken. Collections also include a single isolated cranidium which is slightly smaller, but otherwise similar; this is also presumed to be of degree 4. An impression of an enrolled individual of similar size, is too poorly preserved to reveal its stage of development (Pl. 6, fig. 7). Four slightly larger isolated cephala have a posterior margin to the fringe which becomes directed progressively less anterolaterally, until in the largest individual it is directed transversely (Text-fig. 7). This last form may be a degree five meraspis, but until more specimens showing the number of thoracic segments are available no definite assignment can be made.

A single tiny isolated pygidium (maximum width approximately 2.4 mm ), though poorly preserved, shows a segmented axis and ribbed pleural fields ( Pl . 7, fig. 2). This pygidium is slightly smaller than that of the degree four meraspis and may thus represent an earlier meraspis degree.


A


D

Fig. 7. Diagram illustrating the change in the posterolateral outline of the fringe in meraspides of Bergamia whittardi sp. nov. with increase in size. c. $\times 7$. A based on It. 2763 (Pl. 8, fig. ir) ; B on It. 2765 (Pl. 9, fig. r) ; C on It. 2768 (Pl. 8, fig. 4) ; D on It. 2775 (Pl. 8, fig. 2).

TABLE 20

|  | $\mathrm{A}_{1}$ | B | $\mathrm{I}_{1}$ | K | W | Z | Degree |
| :--- | ---: | :---: | :---: | :---: | :---: | :---: | :---: |
| It. 2772 | - | - | - | - | - | 0.5 | $?$ |
| It. 2763 | - | $c . \mathrm{I} \cdot 2$ | 3.0 | O .8 | - | - | $?$ |
| It. 2773 | - | $c . \mathrm{I} \cdot 2$ | $c .2 .8$ | - | - | - | $?$ |
| It. 2765 | $c .2 .0$ | $c . \mathrm{I} .6$ | - | - | $c .3 . \mathrm{O}$ | 0.5 | 4 |
| It. 2768 | $\mathrm{I} \cdot 8$ | I .5 | 3.7 | $\mathrm{I} \cdot \mathrm{O}$ | - | - | $?$ |
| It. 2775 | I .8 | c. I.5 | 3.0 | 0.8 | - | - | $?$ |
| It. 2774 | $\mathrm{I} \cdot 9$ | I .5 | 3.2 | 0.8 | - | - | $?$ |
| It. 2778 | $\mathrm{I} \cdot 7$ | I .5 | 3.8 | $\mathrm{I} \cdot 3$ | - | - | holaspis |

Dimensions of meraspides and the smallest known holaspis of Bergamia whittardi sp. nov. All measurements in mm. For explanation of symbols see Text-fig. 1 .

Biometrical data. A number of bivariate analyses were undertaken and the results given below. As the majority of data available are from the type locality sample (Pen-cerig Lake quarry), the data given are restricted to this sample.

## TABLE 2I

| x : y | $\overline{\mathrm{x}}$ | var. x | $\overline{\text { y }}$ | var. y | r | $\mathrm{r}_{\mathrm{e}}$ | $\alpha$ | var. $\alpha$ | a | var. a | n |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| $\mathrm{I}_{1}$ : A | 6.42 | $5 \cdot 2870$ | 3.42 | I. 2620 | 0.990 | 0.991 | 0.92 | $0 \cdot 0053$ | 0.49 | 0.00160 | 5 |
| $\mathrm{I}_{1}: B$ | $6 \cdot 48$ | 5.9209 | 2.89 | 1.4622 | 0.971 | 0.974 | I•II | 0.0032 |  | - | 2 |
| A: B | $3 \cdot 38$ | 1.0177 | $2 \cdot 82$ | 0.7017 | 0.997 | 0.997 | 1.00 | 0.0015 | 0.83 | 0.00110 | 6 |
| $\mathrm{B}: \mathrm{B}_{1}$ | 4.13 | 2.9090 | $3 \cdot 27$ | 1.8140 | 0.994 | 0.995 | 1.00 | $0 \cdot 0009$ | 0.79 | 0.00063 | 13 |
| $\mathrm{B}: \mathrm{B}_{2}$ | $4 \cdot 35$ | 2.4918 | $2 \cdot 75$ | r.oris | - $\cdot 990$ | 0.99 I | 1.01 | 0.0019 | 0.64 | 0.00082 | 12 |
| $\mathrm{B}: \mathrm{B}_{3}$ | $4 \cdot 30$ | $2 \cdot 3720$ | I. 82 | $0 \cdot 3737$ | 0.988 | 0.989 | 0.94 | 0.0050 | 0.40 | 0.00095 | 6 |
| $\mathrm{B}: \mathrm{B}_{4}$ | $4 \cdot 22$ | 3.1370 | $2 \cdot 14$ | 0.6280 | 0.968 | 0.971 | 0.89 | 0.0152 | - 45 | 0.00417 | 5 |
| B : K | $3 \cdot 20$ | 2.1153 | 2.22 | $1 \cdot 2703$ | 0.973 | 0.976 | I•II | 0.0022 |  |  | 29 |
| W: Z | $6 \cdot 56$ | 6.9538 | I. 63 | 0.5246 | 0.979 | 0.981 | I $\cdot 10$ | 0.0056 | 0.27 | 0.00039 | 10 |
| W: X | $6 \cdot 56$ | 6.9538 | I-28 | -. 3173 | 0.985 | 0.987 | 1.09 | 0.0039 | $0 \cdot 21$ | 0.00017 | 10 |
| X : Z | I-39 | 0.3341 | 1-79 | 0.5974 | 0.981 | 0.982 | $\mathrm{I}^{1} \mathrm{O} 4$ | 0.0034 | I. 34 | 0.00613 | 13 |

Bivariate statistics for Bergamia whittardi sp. nov. from the type locality. All measurements in mm . For explanation of symbols see Text-fig. I.

## TABLE 22

|  | $\mathrm{R}_{1}$ | Q |
| :--- | ---: | :---: |
| It. 2755 | 4.5 | $\mathrm{I} \cdot 9$ |
| It. 2762 | 8.5 | 2.5 |
| It. 2758 | c. $5 \cdot 7$ | 2.5 |

Details of thoracic measurements for Bergamia whittardi sp. nov. from the type locality.
All measurements in mm . For explanation of symbols see Text-fig. $\mathbf{I}$.

Table 23

| Number of pleural ribs | 3 | 4 |
| :---: | ---: | ---: |
| Number of specimens | 2 | I2 |
| $n=$ I4 |  |  |

Frequency distribution for the number of pleural ribs developed in Bergamia whittardi sp. nov., from the type locality.

## Table 24

| Number of axial rings | 5 | 6 or 7 |  |
| :--- | :--- | :--- | :---: |
| Length of | $0 \cdot \mathrm{I} 9-I \cdot 9 \mathrm{~mm}$ | 5 | 2 |
| pygidial axis | $2 \cdot 0-2 \cdot 7 \mathrm{~mm}$ | 5 | 4 |

Details of the number of axial rings developed in Bergamia whittardi sp. nov. from the type locality sample.

The figures in Table 24 above suggest that for the type locality sample there is possibly a correlation between the size and the number of axial rings developed ( $\mathrm{P}=\mathrm{o} \cdot \mathrm{o6}$ ). This is confirmed by the data for the total known sample of the species where $\mathrm{P}<0.05$.
Discussion. Bergamia whittardi, although closely related to B. prima (Elles) may be readily distinguished from that and all other species assigned to Bergamia by the incomplete $\mathrm{E}_{2}$ arc being developed only anteromedially. It also differs from B. prima in having a slightly higher number of axial rings developed on the pygidium. B. inquilium (Whittard, 1966) is similar in having an incomplete $\mathrm{E}_{2}$ arc, but in this species it is only developed in the posterolateral regions. B. praecedens may also be distinguished by the greater separation of $\mathrm{E}_{1}$ and $\mathrm{E}_{2}$ and by the surface sculpture.

Trinucleinid gen. et sp. indet.
(Pl. 8, fig. 10; Pl. 9, figs 3, 7)

Figured material. It. 2779 (Pl. 8, fig. io) Internal and external moulds of pygidium and posterior part of thorax. It. 2780 (Pl. 9, figs 3, 7) Internal and external moulds of nearly entire specimen.

Locality and horizon. Both specimens occur in the Lower Didymograptus murchisoni shales. Specimen It. 2779 being from the pale ashy shales in the track exposures about sixty yards south-west of Bwlch-y-cefn and It. 2780 from the darker shales of the main tributary to the Howey Brook.

Description. The complete specimen is about 14 mm long, and excluding the fringe, is approximately I 2 mm wide (Pl. 9 , figs 3,7 ). Very little detail is preserved
of the cephalon. The glabella however appears to expand anteriorly as is typical of the trinucleinae. Long curved genal spines extend posteriorly of the pygidium.

The thorax appears to be typically trinucleid.
The pygidium is triangular in outline, just under four times as wide as long. Faint traces of segmentation are visible on the axis and one very weakly developed rib may be present on the pleural fields.

Discussion. These two specimens are worthy of note owing to the extreme rarity of trinucleid remains in the Lower Didymograptus murchisoni shales of the Builth region. The only others known are three fragments of a cryptolithinid. The two specimens described above are here considered as belonging to the same form owing to the similarity of the pygidia and their similar stratigraphical age. Until more complete and better preserved material is available no real comparisons can be made with other forms, though it is noted that $T$. cf. acutofinalis occurs at Builth only a little higher in the succession at the top of the Cwm-Amliw Ash.

## Subfamily CRYPTOLITHINAE Angelin, 1854

## Genus CRYPTOLITHUS Green, 1832

Diagnosis. See page izo.
Type species. Cryptolithus tessellatus Green.
Distribution. The genus is recorded with certainty in the British Isles from the uppermost Llanvirn to Upper Caradoc. In N. America the genus does not appear until the Upper Caradoc (Barnveld of Fisher, I962). The genus is present in the Caradoc and Ashgill of Czechoslovakia (Přibyl and Vaněk, I969) and may also be present in the Caradoc of South-eastern Turkey (Dean, I967).

Discussion. With the inclusion of all the cryptolithinids of the Lower Llanvirn of the Builth district in Bettonia, the earliest known representative of Cryptolithus is from the passage beds at the top of the Betton Beds (top of D. murchisoni Zone) in the Shelve region. There is thus a possibility that Cryptolithus may have developed from Bettonia by the loss of the frontal adventitious pits. The N. American species possess a smaller number of arcs internal to the girder than is typical of the British species and it is thought that further studies may reveal the existence of two or more genera at present placed within Cryptolithus.

## Cryptolithus instabilis sp. nov.

$$
\text { (Pl. 9, figs } 4-6,8 \text {; Pl. Io, figs I-8; Pl. II, figs } 5, \text { I2; Text-fig. 8) }
$$

Diagnosis. Cryptolithus with about thirty pits in the $\mathrm{E}_{1}$ and $\mathrm{I}_{1}$ arcs on each half-fringe; $\mathrm{I}_{1-3}$ continuous medially; $\mathrm{I}_{4}$ generally appearing at row three or four; $I_{5}$ and $I_{6}$ commencing at approximately row eight and twelve. Irregularities in pit arrangement common, particularly in inner I arcs.

Type material. Holotype. It. 2792 (Pl. io, fig. i) Internal mould of cranidium.
Paratypes. It. 2793 (Pl. 9, fig. 4) Mould of ventral surface of lower lamella. It. 2794 (Pl. 9, fig. 5) Internal mould of cranidium with thorax and pygidium folded beneath cephalon. It. 2795 (Pl. II, fig. 5) Internal mould of pygidium. It. 2796 (Pl. Io, fig. 3) Internal mould of nearly complete specimen. It. 2797 (Pl. Io, fig. 4) Internal and external moulds of damaged cranidium. It. 2798 (Pl. Io, fig. 2) Internal mould of damaged cranidium. It. 2799 (Pl. Io, fig. 6) Internal mould of damaged cephalon. It. 2800 (Pl. II, fig. 12) Ventral surface of part of lower lamella. It. 280 I (Pl. 10, fig. 5) Internal mould of damaged cranidium. It. 2802 (Pl. 9, fig. 6) Internal mould of nearly complete specimen. It. 2803 (Pl. Io, fig. 7) Internal mould of nearly complete specimen.

Dimensions of type and figured material.

|  | A | $\mathrm{A}_{1}$ | B | I | $\mathrm{I}_{1}$ | K | $\mathrm{K}_{1}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Holotype | $6 \cdot 6$ | - | $5 \cdot 3$ | $13 \cdot 6$ | II.O | $3 \cdot 0$ | I-2 |
| It. 2793 | - | - | - | c. 12.5 | - | - | - |
| It. 2794 | - | - | c. $6 \cdot \mathrm{I}$ | - | c. II• 2 | - | - |
| It. 2796 | c. $7 \cdot 5$ | - | c. $6 \cdot \mathrm{I}$ | - | 12.5 | - | - |
| It. 2797 | c. $5 \cdot 7$ | - | c. 4.7 | - | - | - | - |
| It. 2798 | $7 \cdot 9$ | - | $6 \cdot 4$ | - | 12.5 | $3 \cdot 5$ | - |
| It. 2799 | $8 \cdot 8$ | - | $6 \cdot 8$ | - | - | $3 \cdot 0$ | - |
| It. 2801 | 6-I | $6 \cdot 7$ | - | - | - | $3 \cdot 1$ | - |
| It. 2802 | - | - | $4 \cdot 0$ | - | - | - | I.4 |
| It. 2803 | $7 \cdot 2$ | - | $5 \cdot 4$ | - | $12 \cdot 2$ | $3 \cdot 0$ | I'5 |
| It. 2804 | $8 \cdot 2$ | - | $6 \cdot 5$ | 17.5 | 12.5 | $3 \cdot 6$ | I 7 |
| It. 2805 | $6 \cdot 2$ | - | $5 \cdot 0$ | - | $9 \cdot 7$ | $2 \cdot 7$ |  |


|  |  |  | No. of |  | No. of ribs |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
| It. 2795 | W | X | Z | axial rings | Left | Right |
| It. 2802 | $9 \cdot 8$ | $\mathrm{I} \cdot 6$ | $2 \cdot 8$ | Io+ | 5 | 5 |
|  | $8 \cdot 0$ | $\mathrm{I} \cdot 4$ | $2 \cdot 0$ | - | 5 | 5 |

All measurements in mm. For explanation of symbols see Text-fig. r. Note B-glabellar length, is measured from the anterior of the pre-glabellar field.

Type locality and horizon. The holotype and paratypes It. 2793-2799 are from the Llandeilo shales exposed in the left bank of the Dulas Brook, 60 yds north of spot height 727 , I50 yds south-west of the old quarry 350 yds west of Maesgwynne. Paratypes It. 2800-2803 are from shales of similar age exposed at the easterly end of the stream section 160 yds south-east of Tre coed.

Other figured material. It. 2804 (Pl. io, fig. 8); It. 2805 (Pl. 9, fig. 8).
Distribution. The species is known with certainty only from the two localities yielding the type specimens, although it is probably present in the stream section

I5 yds south-west of the quarry at Maesgwynne, and in the lane leading to Newmead, but preservation at these latter localities is not good enough to allow positive identification.

Description. Excluding the fringe and genal spines, complete individuals are roundly rectangular in outline, being slightly longer than wide.

The cephalon is approximately semicircular with no marked angulation anterolaterally. The clavate, convex glabella commonly has a low median ridge extending behind a small median glabellar node. Three pairs of lateral glabellar furrows are present, generally taking the form of shallow, oval depressions on the sides of the glabella (Pl. 9, fig. 6). In some cases, however, the furrows appear much deeper, but this is attributed to distortion (Pl. Io, fig. 2). Suggestions of weakly developed alae are present in a few specimens (Pl. Io, fig. 3). Anteriorly the glabella is truncated rather squarely by a shallow preglabellar furrow separating the glabella from a narrow ribbon-shaped preglabellar field.

The occipital furrow is shallow and broad medially, deepening laterally into deep occipital pits. The occipital ring consists of little more than an expanded base to a well developed occipital spine.

Anteriorly the axial furrows are deep and narrow, with well developed fossulae, which are bounded anteriorly by a ridge linking the genal regions and the preglabellar field, thus terminating the axial furrows behind the fringe. The furrows are gently curved and become shallower and wider to the posterior.

The genal regions are quadrant-shaped and only gently convex. Some specimens show traces of two thin simple genal caecae on the external surface of the genae (Pl. Io, figs 6, 7). The external surface of both the genae and glabella is covered with numerous small pits ( Pl . Io, fig. 4). No eye tubercles or ridges are developed. The posterior border furrow is straight, wide and shallow; lateral pits appear not to be developed.

Internally the lateral glabellar furrows are developed as slightly raised areas, while apodemes correspond to the anterior fossulae. No trace of the median glabellar node or median ridge has been detected on internal moulds.

Full details of the fringe are not known due to the lack of really well-preserved material. In general character, the fringe is of typical cryptolithid-type with a strong $I_{1-2}$ ridge on the upper lamella; slightly larger $E_{1}$ and $I_{1}$ pits and a basic radial arrangement of the pits of all arcs. A characteristic feature of the species is the frequent irregularities of pit distribution.

There are between twenty-seven and thirty pits in the $E_{1}$ and $I_{1}$ arcs on each halffringe, the total number of which, as far as can be ascertained front the limited amount of material available, is not dependent on the size of the individual. Posterolaterally, auxilliary pits are commonly developed in the $\mathrm{E}_{1}$ arc (Pl. Io, fig. I). The inner arcs are not well known, but anteriorly all the pits show a basic radial arrangement ; laterally this radial pattern is lost due to the development of auxiliary pits in the inner arcs. The development of these extra pits appears to follow no set pattern, nor is their arrangement typically symmetrical. In general the arcs $I_{1-3}$ are continuous anteriorly, though in about one-fifth of the specimens the $I_{3}$ arc is absent
in row $\mathrm{I} . \mathrm{I}_{4}$ generally commences at row 3 , but in a few cases it appears in row 2 , 4 or 5 (see Table 25). Laterally arcs $\mathrm{I}_{5}$ and $\mathrm{I}_{6}$ commence at about row 8 and 12 respectively.

The genal flanges are well developed, extending a short distance behind the posterior margin of the cephalon. Between sixty and seventy irregularly placed pits are developed on each flange. In many specimens the inner portion of the ridge separating rows five and six is markedly swollen causing some distortion in the general radial pattern present anteriorly (Pl. 10, figs $\mathrm{I}, 7$ ). On the lower lamella the girder is only slightly more strongly developed than the pseudogirders separating the various I arcs. The pseudogirders and girder bear terrace lines on the outer surface. Two specimens, It. 2804 (Pl. Io, fig. 8) and It. 2805 (Pl. 9, fig. 8) are provisionally included in this species although they show slight differences in that they have a single pit of the $E_{1}$ arc situated on the sagittal line. It. 2804 also shows considerable amount of irregularity in the development of the inner I arcs, particularly laterally. The marginal facial suture is only rarely observed (Pl. ro, figs 2,8 ). The proximal end of the genal spines are directed more or less posteriorly, the distal ends being unknown.

The thorax is rectangular and of typical trinucleid morphology.
The triangular pygidium is about three times as wide as long. The convex axis has at least ten axial rings, whilst the pleural fields are gently undulate with a narrow border, five or six ribs and a small terminal area. The ribs are directed somewhat posteriorly, this deflection being increased distally. The number of ribs developed is not related to the pygidial length (see Table 27).


Fig. 8. Reconstruction of the cephalon of Cryptolithus instabilis sp. nov. in dorsal view. c. $\times 6$.

Biometrical data.

## TAble 25

$$
\text { Commencing row of arc } \mathrm{I}_{4}
$$

left half-fringe
right half-fringe

| 3 | 3 | 4 | 4 | 3 | 3 | 3 | - |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | ---: |
| 2 | 3 | 4 | - | 3 | 3 | - | 5 |

Details of the row in which $I_{4}$ arc commences in eight specimens of Cryptolithus instabilis sp. nov.

Table 26

| x : y | $\overline{\mathrm{x}}$ | var. x | $\overline{\text { y }}$ | var. y | r | $\mathrm{r}_{\mathrm{e}}$ | $\alpha$ | ar. $\alpha$ | a | var. | n |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| $\mathrm{I}_{1}$ : A | 10.92 | $6 \cdot 3644$ | $6 \cdot 33$ | 3.3800 | 0.917 | 0.920 | $1 \cdot 25$ | 0.0341 | 0.73 | -0.01208 | 9 |
| $\mathrm{I}_{1}: \mathrm{B}$ | 11.60 | 5.1727 | $5 \cdot 75$ | I.8191 | 0.917 | 0.919 | I•19 | . 0221 | 0.59 | 0.00560 | 12 |
| A : B | $7 \cdot 17$ | I.9635 | $5 \cdot 78$ | I. 3603 | 0.966 | 0.967 | I. 03 | 0.0054 | 0.83 | -0.00356 | 15 |
| B : K | $5 \cdot 79$ | I 2942 | 3.07 | $0 \cdot 3391$ | 0.902 | 0.903 | 0.97 | 0.0096 | 0.51 | 0.00272 | 20 |
| W: Z | 9.48 | 4.0836 | 2.82 | 0.5776 | 0.927 | -930 | I. 26 | 0.0237 | 0.38 | .00220 | 11 |
| W: X | $9 \cdot 86$ | 3.7754 | 1.57 | 0.1861 | 0.918 | 0.921 | 1.38 | 0.0290 |  |  | 12 |
| X : Z | I•57 | 0.145 I | 3.04 | 0.4482 | 0.853 | o.856 | 0.91 | 0.01 | 1.76 | 0.04207 | 22 |

Bivariate statistics for Cryptolithus instabilis sp. nov. for the total sample from the inlier. All measurements in mm. For explanation of symbols see Text-fig. I. Note that B - 'Glabellar length' is here taken from the anterior of the preglabellar field.

## TAble 27

| Number of ribs |  | 5 | 6 |
| :--- | ---: | :--- | :--- |
| Pygidial length | $2 \cdot 4-3 \cdot 0$ | 2 | 2 |
| in mm | $3 \cdot \mathrm{I}-3 \cdot 9$ | 4 | I |
|  | $\mathrm{n}=9$ |  |  |

Details of the number of ribs developed on the pygidium of Cryptolithus instabilis sp. nov. for the total sample.

Discussion. The species, erroneously recorded as Trinucleus (Cryptolithus) lloydi (Murchison, 1839) by Elles (1940), is closely related to the Llandeilian cryptolithinids from the Shelve area. From Cryptolithus inopinatus Whittard, 1958 it is easily distinguished by the absence of the $\mathrm{I}_{4}$ arc medially and the delayed appearance of pits of the $I_{5}$ arc to about row eight. Cryptolithus intertextus Whittard, 1958 differs in that the radial arrangement of the pits is rapidly lost laterally due to the intercalation of interradial rows in the arcs $\mathrm{I}_{2-4}$. Also, as in C. inopinatus, there are fewer pits of the $\mathrm{I}_{4}$ arc absent medially than in C. instabilis, while the cephalon of $C$. intertextus is relatively longer (sag.). Of all the Shelve cryptolithinids, C. radiatilis Whittard is perhaps the most closely related to C. instabilis, although it may be distinguished by the appearance of the $I_{4}$ arc in row one or two and by its apparent lack of the $I_{6}$ arc. Furthermore C. vadiatilis appears not to
attain the dimensions reached by C. instabilis, and the outline of the cephalon is less rounded. C. abductus Přibyl and Vaněk, 1969 , which was considered closely related morphologically to $C$. radiatilis by Přibyl and Vaněk, presumably chiefly on account of its well-developed radial arrangement of pits which persists to the posterior margin of the fringe, is readily distinguished by the presence of $\mathrm{E}_{2}$ arc, lack of arcs $\mathrm{I}_{5-6}$ and fewer pits in each arc.

## Cryptolithus sp. A

## (Pl. II, figs $I, 4,6$ )

Figured material. It. 2806 (Pl. it, fig. I) Mould of part of dorsal surface of lower lamella. It. 2807 (Pl. II, fig. 4) Internal mould of pygidium. It. 2808 (Pl. II, fig. 6) External mould of part of thorax.

Locality and horizon. Near the base of the Lower Didymograptus murchisoni shales on the right bank of the stream flowing north-west from the pass above Bwlch-y-cefn, about 100 yds downstream from the waterfall.

Description. The three figured specimens are the only trinucleid fragments known from the locality and are assumed to belong to a single species. The fragment of the lower lamella reveals that the $\mathrm{E}_{1}$ and $\mathrm{I}_{1-3}$ arcs are present, as is a strong girder and a well-developed pseudogirder between $I_{1}$ and $I_{2}$; both girder and pseudogirder bear terrace lines. Approximately twenty-five pits are present in the $\mathrm{E}_{1}$ arc on the left half-fringe (right in ventral view), but the preservation does not allow an accurate count. The pits of the genal flange are smaller than the others. Long gently curved genal spines are developed. Although the preservation is rather poor, the thorax is seemingly typically trinucleid. The pygidium is triangular in outline being three and a half times as wide as long. At least six ribs are developed on the pleural fields and seven axial rings are clearly visible on the axis.

DISCUSSION. If these specimens are correctly placed in Cryptolithus then they are of particular interest for they are probably slightly older than the previous oldest known member of the genus recorded from strata below the top of the Upper Llanvirn of the Shelve region by Whittard (1958, pp. 7I ff.).

## ? Cryptolithus sp. B

(Pl. II, figs 2, 7)
Figured specimen. It. 2809 Fragment of lower lamella.
Locality and horizon. Stream section east of Wellfield Lodge, east of the main road, immediately above the point where the stream is piped under the road; shales assigned to the G. teretiusculus Zone.

Description. A single fragment of a lower lamella shows only the $\mathrm{E}_{1}, \mathrm{I}_{1}$ and $\mathrm{I}_{2}$ arcs. The $I_{1}$ and $I_{2}$ arcs are separated by a strong pseudogirder which is only slightly
less prominent than the girder; both girder and pseudogirder bear terrace lines. A unique feature seen in this specimen is the arrangement of the pits in the $I_{1}$ arc (Pl. II, fig. 7), where laterally alternate pits have been pushed outwards as if by overcrowding. The genal flange is irregularly pitted with pits slightly smaller than those in the arcs.

Discussion. A further specimen of ?Cryptolithus is known from shales from the other side of the road, and while it is quite possible that this is conspecific with ?Cryptolithus sp. B, it is here described separately as ?Cryptolithus sp. C until more material is available.
?Cryptolithus sp. C
(Pl. II, figs 3, 8)
Figured specimen. It. 28io External mould of fragment of cephalon.
Locality and horizon. Stream section at Wellfield Lodge immediately downstream of the point where the stream emerges after being piped under the road; shales assigned to the $G$. teretiusculus Zone.

Description. A single fragmentary specimen is of note in that of the arcs apparently internal to the girder, only the $I_{1}$ and $I_{2}$ arcs are continuous medially. The $\mathrm{I}_{3}$ arc does not commence until row three; $\mathrm{I}_{4}$ beginning at about row eight or nine. In this respect it is not unlike Bettonia chamberlaini (Elles) from the Llanvirn, although no adventitious pits are present medially.

Until the position of the girder is definitely known it is impossible to place this form generically with any certainty. Further the lack of any frontal adventitious pits suggests it belongs to Cryptolithus, their absence does not necessarily preclude it from Bettonia.

Discussion. Two further trinucleids are known from this locality; one, It. 2830 appears to have some affinity to Bettonia superstes Whittard, the other is too poorly preserved to be generically placed.

Genus BETTONIA Whittard, 1956
Diagnosis. See page izo.
Type species. Trinucleus chamberlaini Elles, 1940.
Distribution. Known from the upper beds of the Lower Llanvirn D. bifidus Zone; D. speciosus subzone) and the Llandeilo (G. teretiusculus Zone) of the Builth region; from the Weston and the Betton Beds (D. murchisoni Zone) and possibly also from the Meadowtown Beds (G. teretiusculus Zone) of the Shelve area.

Discussion. Whittard originally erected this genus to accommodate five or six poorly known species which were superficially similar to Cryptolithus Green, 1832, but differed in that they possessed a varying number of adventitious pits
external to the $E_{1}$ arc. In the description of his type species, Bettonia frontalis Whittard, 1956, he acknowledged that it was very like 'Trinucleus' (Cryptolithus) gibbosus Elles, 1940, from Builth and that differences, if any, were only likely to be found in the number and arrangements of the adventitious pits. He referred both T. (C.) gibbosus and T. chamberlaini to Bettonia.

The study of a large amount of material from the type locality of Bettonia chamberlaini (Elles, 1940) and B. gibbosa has shown these two species to be identical. Furthermore, the population exhibits considerable variation both in arrangement and number of pits in the $E_{1}$ and $I_{1}$ arcs frontally and in the number of adventitious pits developed which ranges from $0-10$ (see Text-fig. Io), which covers a greater range than that exhibited by all five of Whittard's original species with the exception of Bettonia superstes. The variation found in the anteromedian distribution of the pits of the $\mathrm{E}_{1}$ and $\mathrm{I}_{1}$ arcs in $B$. chamberlaini together with $B$. frontalis, $B$. irregularis Whittard and $B$. paucipuncta Whittard may be considered as a basically simple radial pattern in which one or more pits may become slightly displaced (see Text-figs Io, II). In view of the variation now known to be present within a single population of Bettonia, B. frontalis, B. irregularis, B. paucipuncta together with B. gibbosa are here considered as junior synonyms of Bettonia chamberlaini (Elles, 1940).

The occurrence within the sample of the population of $B$. chamberlaini of individuals with no adventitious pits, and others with one or two pits only on one half of the fringe raises the question of the validity of the genus Bettonia as distinct from Cryptolithus. Further doubt is raised by the similarity, apart from the frontal adventitious pits, between Cryptolithus intertextus Whittard, 1958, and Bettonia superstes Whittard, I956. However, until more samples are available, the genus Bettonia is provisionally retained for forms in which the majority of individuals have adventitious pits developed, whilst Cryptolithus rarely, if ever, has them. Cryptolithus sp. Whittard (1956: 68, pl. 9, fig. 16) is considered to belong to $B$. chamberlaini. It is thought that $B$. superstes might be better considered as being conspecific with C. intertextus, if this is so it would then leave $B$. chamberlaini as the sole representative of the genus Bettonia.

## Bettonia chamberlaini (Elles)

(Pl. II, figs 9-II, I3-I5; Pl. I2, figs I-7; Pl. I3, figs $I-8$; Pl. I4, figs $I-5,8-10$; Text-figs 9-II)
1940 Trinucleus chamberlaini Elles: 423-424, pl. 29, figs 10-12, non fig. 13 which is T. abruptus. 1940 Trinucleus (Cryptolithus) gibbosus Elles: 425-426, pl. 31, figs 3-9.
194I 'Tvinucleus' chamberlaini Elles; Whittington: 26.
1941 'Trinucleus' (Cryptolithus) gibbosus Elles; Whittington: 26.
194I Cryptolithus? chamberlaini (Elles); Lamont: 449.
1941 Cryptolithus gibbosus Elles; Lamont: 464.
1956 Bettonia frontalis Whittard: $67-68$, pl. 9, fig. 7.
1956 Bettonia chamberlaini (Elles); Whittard: 67, 69, pl. 9, figs 13, 14.
1956 Bettonia gibbosa (Elles); Whittard: $67-70$, pl. 9, fig. 8.
1956 Cryptolithus sp. Whittard: 68, pl. 9, fig. 16.

1956 Bettonia paucipuncta Whittard: 68-69, pl. 9, figs 9-11.
1956 Bettonia irregularis Whittard: 69-70, pl. 9, fig. 12.
1966 Bettonia frontalis Whittard; Whittard: 280-281, pl. 49, figs 1-4.
Diagnosis. Bettonia with nil to ten frontal adventitious pits external to $\mathrm{E}_{1}$ arc, with rare development of pits external to $\mathrm{E}_{1}$ posterolaterally. Arcs $\mathrm{E}_{1}, \mathrm{I}_{1-2}$ continuous with about twenty pits in $E_{1}$ and $I_{1}$, and fifteen in $I_{2}$, on each half-fringe; $I_{3}$ generally appears in row two or three and contains about fourteen pits; $\mathrm{I}_{4}$ commencing between row four and twelve, consists of a variable number of small pits adjacent to genae. Median pit in $\mathrm{E}_{1}$ always present though commonly displaced; auxiliary pits in $\mathrm{E}_{1}$ commonly developed, but rare in other arcs. Pygidium triangular; axial rings exceed in number the weakly developed ribs.

Type material. Holotype. BU 26ia (Chamberlain Collection) (PI. I2, fig. 5) Internal mould of nearly complete specimen.

Paratypes. BU 262 (Chamberlain Collection) (Pl. I3, fig. 4) Internal mould of cranidium, pygidium and part of thorax. BU 263 (Chamberlain Collection) (Pl. I2, fig. I) Internal mould of damaged nearly complete specimen.

Dimensions.

|  | A | B | $\mathrm{B}_{1}$ | $\mathrm{B}_{2}$ | $\mathrm{I}_{1}$ |  | $\mathrm{K}_{1}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Holotype | c. $5 \cdot 8$ | c. $4 \cdot 6$ | $3 \cdot 8$ | $3 \cdot 0$ | - |  |  |
| BU 262 | c. 7.5 | c. $5 \cdot 9$ | $4 \cdot 7$ | $3 \cdot 6$ | 10.0 |  | I. 8 |
| BU 263 | - | $3 \cdot 8$ | - | - | - |  | - |
|  |  |  |  | No. of |  | No. | ribs |
|  | W | X | Z | axial rings |  | Left | Right |
| Holotype | $8 \cdot 2$ | I. 6 | $2 \cdot 3$ | ? |  | - | - |
| BU 263 | c. $6 \cdot 2$ | I•3 | I. 6 | ? |  | trace | trace |

All measurements in mm. For explanation of symbols see Text-fig. 1 .
Fringe Data. Paratype BU 262

Numbers of pits in various arcs

|  | $\mathrm{E}_{1}$ | $\mathrm{I}_{1}$ | $\mathrm{I}_{2}$ | $\mathrm{I}_{3}$ | $\mathrm{I}_{4}$ |
| :--- | :---: | :--- | :--- | :--- | :--- |
| Left half-fringe | 22 | I 8 | I 6 | I 4 | $\mathrm{I} 0+$ ? |
| Right half-fringe | $22+$ | $\mathrm{I} 6+$ | I 6 | I 3 | IO |

$\mathrm{E}_{1}, \mathrm{I}_{1-2}$ are continuous; $\mathrm{I}_{3}$ commences at row two ; $\mathrm{I}_{4}$ at row three. Five anterior adventitious pits are developed. Auxiliary pits $e_{1}$ xiii, and xiv are present on both left and right half-fringes. Fifteen radial rows are developed on the left half-fringe and at least fourteen on the right.

Only a fragment of the fringe is preserved in the holotype and no data are available. Fringe details are not available in the second paratype.

Type locality and horizon. All three type specimens are from the shales of Lower Llanvirn age in the cliff section on the left bank of the Howey Brook, half a mile east-south-east of Carregwiber.

Other figured material. It. 28II (Pl. I4, fig. Io) ; It. 28 I 2 (Pl. il, fig. I5; Pl. I4, fig. I) ; It. 28ı3 (Pl. I2, fig. 7) ; It. 28I4 (Pl. I2, fig. 6) ; It. 28I5 (Pl. II, fig. Io); It. 28 I 6 (Pl. II, fig. 14) ; It. 28 I 7 (Pl. I2, fig. 2) ; It. 28 I 8 (Pl. I2, fig. 4) ; It. 28 I 9 (Pl. I3, fig. 3) ; It. 2820 (Pl. I3, fig. 7) ; It. 282 ( Pl. I3, fig. 6) ; It. 2822 (Pl. I4, fig. 2) ; It. 2823 (Pl. I3, fig. 8) ; It. 2825 (Pl. II, fig. II) ; It. 2826 (Pl. II, fig. 9) ; It. 2827 (Pl. II, fig. I3) ; It. 2828 (Pl. I4, fig. 4) ; It. 2829 (Pl. I4, fig. 5) ; GSM 86785 (Pl. I2, fig. 3) ; GSM 86786A (Pl. I4, fig. 8) ; GSM 86789 (Pl. I4, fig. 3) ; SM A 10082 (Pl. I3, fig. 5) ; BU 26Ib (Pl. I3, fig. I) ; BU 264 (Pl. I3, fig. 2) ; BU 368 (Pl. 14, fig. 9).

Distribution. The species is known from the upper beds of the Lower Llanvirn (D. speciosus Subzone) of the Builth region; and from the Betton and the Weston Beds ( $D$. murchisoni Zone) of the Shelve area. In the Builth region it is very abundant at the type locality and relatively common at the small quarries 600 yds east of Upper Gilwen; it also occurs at various other localities at the same horizon in the Builth inlier.

Description. Excluding the genal spines and the fringe, complete specimens are roundly quadrate in out line.

The cephalic outline varies between semicircular and subrectangular, with the anterolateral angulation being variably developed. Excluding the occipital spine, the cephalon is generally about twice as wide as long.

The pyriform glabella is strongly convex and elevated well above the genal regions. In undeformed specimens it is generally about twice as long as wide. Three pairs of short lateral glabellar furrows typically take the form of rather indistinct shallow depressions on the near vertical sides of the glabella. The anterior pair occur at about two-fifths, the median pair at three-fifths and the posterior pair at about four-fifths along the glabella, measured from the anterior. Rarely a small median glabellar node is preserved in internal moulds (Pl. 13, fig. 7) ; apparently no such node is developed on the dorsal surface (Pl. I2, fig. 4). Commonly external moulds fail to show any surface markings, however, a few well-preserved specimens, particularly small holaspides, show a coarse reticulation on the glabella, and a slightly less coarse development on the genae (Pl. 12, fig. 4; Pl. 14, fig. 4).

The occipital ring forms an expanded base to the well-developed occipital spine (Pl. I2, fig. 4). The occipital furrow deepens laterally to form deep occipital pits which are directed anterolaterally.

The axial furrows, deep anteriorly with well-developed anterior fossulae, follow the lateral margins of the glabella closely becoming wider posteriorly. Alae are not developed.

The genae are quadrant-shaped with the inner margin gently concave and the posterior margin directed slightly anteriorly. They are moderately convex with fairly steeply sloping outer regions. Occasional specimens (BU 262, Pl. 13, fig. 4) show two faint caecae directed posterolaterally across the gena from about the mid-
point of the inner margin towards the genal angle. The posterior border furrow is straight, broad and fairly shallow and has no lateral pit.

Internally the lateral glabellar furrows form poorly developed raised platforms. A small apodeme corresponds to each of the anterior fossulae.

The hypostoma is not known.
In spite of commonly developed cracks on the fringe of many specimens, particularly around the margins of the genae, it seems that the genal roll was moderately steeply declined, and the brim relatively flat; the change in curvature of the upper lamella probably being located along the strong ridge between $\mathrm{I}_{1}$ and $\mathrm{I}_{2}$. The fringe is of constant width with a short tongue extending behind the genae, lateral to the fulcrum. Five arcs of pits, $\mathrm{E}_{1}, \mathrm{I}_{1-4}$, are developed. The pits of the various arcs are arranged essentially radially, except near the genal angles, with the pits of $E_{1}$ and $I_{1}$ being larger than the remainder. The $E_{1}, I_{1-2}$ arcs are continuous; $\mathrm{I}_{3}$ arc generally commences at either row two or three and $\mathrm{I}_{4}$ appears somewhat variably between row four and twelve. Generally about fifteen radial rows are developed on each half-fringe, with the anterolateral angulation occurring, if present, at about row twelve. Anteromedially the rows of pits diverge slightly and a median pit is present in the $\mathrm{E}_{1}$ arc. Variations in the pattern of pits are common, and are caused by the displacement of one or more pits; they may all be referred to the basic pattern however (see Text-figs io, II). The number of anterior adventitious pits external to $\mathrm{E}_{1}$ varies from nil to ten, and they are rarely distributed symmetrically with respect to the sagittal line. Rarely adventitious pits are also located


Fig. 9. Reconstruction of the cephalon of Bettonia chamberlaini (Elles) in dorsal view. c. $\times 8$.


A


D


G


B


E


H


C


F


I

Fig. 1o. Diagram illustrating the variation in numbers and distribution of pits in the anteromedian portion of the fringe in Bettonia chamberlaini (Elles) from the type locality. The diagrams are arranged showing a progressive increase in the number of anterior adventitious pits (shown as solid circles) present external to the $\mathrm{E}_{1}$ arc. The median pit of the $\mathrm{E}_{1}$ arc, at times displaced laterally, is arrowed. All diagrams $\times 7$. AIt. 2820 (Pl. 13, fig. 7) ; B-BU 261a (Pl. 12, fig. 5); C-It. 2821 (Pl. 13, fig. 6); DBU 26 rb (Pl. 13, fig. 1) ; E—It. 2813 (Pl. 12, fig. 7) ; F-BU 264 (Pl. 13, fig. 2); GBU 262 (Pl. 13, fig. 4) ; H—It. 2817 (Pl. 12, fig. 2) ; I-It. 2819 (Pl. 13, fig. 3).


A


B


C

Fig. if. Diagram illustrating the variation in numbers and distribution of pits in the anteromedian portion of the fringe in the type specimens of Whittard's species Bettonia paucipuncta, Bettonia irregularis and Bettonia frontalis from Shropshire. Anterior adventitious pits shown as solid circles. The median pit of the $E_{1}$ arc, at times displaced laterally, is arrowed. Note that all these distributions fall within the variation shown in Fig. io for the type locality sample of Bettonia chamberlaini (Elles). All diagrams $\times 7$. A-GSM 86786A B. 'paucipuncta' (Pl. 14, fig. 8); B-GSM 86789 B. 'irvegularis' (Pl. 14, fig. 3) ; C-GSM 86785 B. 'frontalis' (Pl. 12, fig. 3).
posterolaterally external to $\mathrm{E}_{1}$ (Pl. 12, fig. 2); auxiliary pits are common in the $\mathrm{E}_{1}$ arc, much less frequent in $I_{1}$ and rare in the other arcs. The auxiliary pits are rarely symmetrically distributed. The genal flanges lack a radial pit arrangement and although some variation is found, the arrangement is typically like that of Text-fig. 9. Occasional abnormalities of pit distribution usually take the form of a slight distortion of the radial pattern. One individual (Pl. I4, fig. 2) however has an $E_{1}$ pit missing laterally on both halves of the fringe.

The pit distribution on the lower lamella corresponds with that of the upper lamella. A strong, apparently smooth girder merges posterolaterally with the base of the genal spines; the ridge between $I_{1}$ and $I_{2}$ is represented ventrally by a pseudogirder, which may be as strongly developed as the girder, and shows faint traces of terrace lines (Pl. I4, fig. I).

No correlation exists between the size of individuals and the number of pits present in any arc, or the number of anterior adventitious pits present; neither is there any correlation between size and the number of radial rows developed, nor in the commencement of the $I_{2}$ and $I_{3}$ arcs (for full fringe data see pages $\mathrm{r} 65-6$ ).

The genal spines are long, slender and gently incurved, extending some way behind the pygidium.

The suture line is not seen in the Builth material, but is clearly visible on GSM 86786A (Pl. I4, fig. 8), from Shelve (the original holotype of B. paucipuncta), where it passes round the declined marginal band and continues along the posterior margin of the cephalon, disappearing near the fulcrum.

The thorax is of normal trinucleid pattern and requires no detailed description. It is about two and a half times as wide as long, the maximum width occurring at the third segment. The axis occupies about two-fifths of the total thoracic width anteriorly, tapering slightly to the rear.

The triangular pygidium is about two and three-quarter times as wide as long, with a straight anterior margin, (excluding the articulating half-ring), and steeply declined smooth posterior and lateral borders. The inner margin of the posterior border is defined by a low narrow rim. The moderately convex tapering axis occupies slightly less than one-fifth of the anterior width of the pygidium. Traces of axial rings are seen in some specimens and up to eight are known. The axial furrows converge slightly, and become weaker to the posterior. The flat pleural fields have an anterior border and one, or possibly two, very weakly developed ribs.

Ontogeny. Although several specimens smaller than the smallest certain holaspis are known, the preservation is such that the number of thoracic segments developed cannot be precisely determined. All these small specimens, whether they are meraspides or small holaspides, resemble adult specimens except in size.

Biometrical data. Although the species is extremely abundant at the type locality, the specimens are so closely packed together that they overlap and crush one another thus making measurements impossible on the majority of specimens. However some data are available for a moderately sized sample and these are given below in Tables 28-35.

Table 28


Frequency distributions for the number of pits developed in arc $\mathrm{E}_{1}$ for Bettonia chamberlaini (Elles) from the type locality.

Table 29
$\begin{array}{lllll}\text { Row in which } \mathrm{I}_{3} \text { first appears } & 2 & 3 & 4 & 5\end{array}$
Number of specimens $\quad$ I8 $78 \quad 2 \quad 1 \quad(n=28)$
Frequency distribution for the commencement of arc $\mathrm{I}_{3}$ in Bettonia chamberlaini (Elles) from the type locality. Arcs $\mathrm{E}_{1}, \mathrm{I}_{1-2}$ are continuous anteromedially.

Table 30
Row in which $\mathrm{I}_{4}$ first appears
Number of specimens

$$
\begin{array}{rrrrrrrrrr}
4 & 5 & 6 & 7 & 8 & 9 & \text { Io } & \text { II } & \text { I2 } & \\
\mathrm{I} & \mathrm{I} & - & \mathrm{I} & \mathrm{I} & \mathrm{I} & \mathrm{I} & - & \mathrm{I} & (\mathrm{n}=7)
\end{array}
$$

Frequency distribution for the commencement of arc $\mathrm{I}_{4}$ in Bettonia chamberlaini (Elles) from the type locality.

## Table 3i

Row
Number of specimens

Io II I2 I3 rounded outline $\begin{array}{lllll}2 & 2 & 5 & 4 & 4\end{array}$

Frequency distribution for the position of the anterolateral angulation where present in Bettonia chamberlaini (Elles) from the type locality sample.

Table 32
$\begin{array}{lllllllllllll}\text { Number of pits } & 0 & \text { I } & 2 & 3 & 4 & 5 & 6 & 7 & 8 & 9 & \text { Io } & \\ \text { Number of specimens } & 2 & \text { I } & \text { I } & \text { I } & \text { I } & 4 & \text { I } & \text { I } & \text { I } & - & \text { I } & (\mathrm{n}=14)\end{array}$
Frequency distribution for the number of anterior adventitious pits developed in Bettonia chamberlaini (Elles) from the type locality sample.

## Table 33

| Number of radial rows | I4 | I5 | I6 | I7 |  |
| :--- | ---: | ---: | ---: | ---: | :--- |
| Number of specimens | 2 | 4 | I | I | $(\mathrm{n}=8)$ |

Frequency distribution for the number of radial rows developed in Bettonia chamberlaini (Elles) from the type locality sample.

In all the above fringe data the half-fringe is taken as that part of the fringe to the left or right of the median pit in the $\mathrm{E}_{1}$ arc. In half-fringe counts on the $\mathrm{E}_{1}$ arc the median pit is not included. In some specimens a small error may be introduced by the incorrect determination of the median pit. Such errors are small and tend to cancel out in the overall data from the sample.

## Table 34

| x : y | $\overline{\mathrm{x}}$ | var. x | $\bar{y}$ | var. y | r | $\mathrm{r}_{\mathrm{e}}$ | $\alpha$ | var. $\alpha$ | a | var. a | n |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| $\mathrm{I}_{1}$ : A | 8.16 | I.9346 | 5•74 | I. 2082 | 0.889 | 0.890 | I-12 | 0.0096 | $0 \cdot 79$ | $0 \cdot 00486$ | 29 |
| $\mathrm{I}_{1}: \mathrm{B}$ | 8.17 | $2 \cdot 5038$ | 4.44 | 0.8664 | 0.886 | 0.888 | I. 08 | $0 \cdot 0045$ | $0 \cdot 59$ | 0.00136 | 57 |
| A : B | $5 \cdot 76$ | I.1479 | $4 \cdot 53$ | 0.7179 | 0.977 | 0.977 | I $\cdot 00$ | 0.0013 | 0.79 | 0.00081 | $3^{8}$ |
| $\mathrm{B}: \mathrm{B}_{1}$ | 4.71 | 0.5007 | $3 \cdot 76$ | $0 \cdot 3888$ | 0.895 | - 0.896 | I-10 | 0.0199 | 0.88 | 0.01286 | 14 |
| $\mathrm{B}: \mathrm{B}_{2}$ | $4 \cdot 74$ | 0.6365 | $2 \cdot 96$ | 0.2265 | 0.962 | 0.963 | $0 \cdot 95$ | $0 \cdot 0074$ | $0 \cdot 60$ | $0 \cdot 00292$ | I I |
| $\mathrm{B}: \mathrm{K}$ | 4.34 | 0.9990 | $2 \cdot 35$ | -.3134 | 0.88 I | 0.884 | [.O3 | 0.0036 | 0.56 | $0 \cdot 00108$ | 67 |
| $\mathrm{K}: \mathrm{K}_{\mathrm{I}}$ | 2.49 | $0 \cdot 2807$ | I. 44 | 0.0885 | $0 \cdot 765$ | 0.769 | 0.97 | $0 \cdot 0099$ | $0 \cdot 56$ | 0.00335 | 41 |
| W : Z | 6.41 | 1.9128 | 1.78 | o.1689 | - $\cdot 864$ | 0.866 | I. 07 | -.0178 | $0 \cdot 30$ | $0 \cdot 00140$ | 18 |
| W : X | 6.41 | 1.9128 | I. 23 | 0.0835 | 0.905 | 0.908 | I. 08 | 0.0129 | $0 \cdot 21$ | $0 \cdot 00049$ | 18 |
| X : Z | I $\cdot 23$ | 0.0704 | I-78 | -.1654 | - 0.887 | -0.889 | I. 06 | 0.0112 | I. 53 | 0.02390 | 23 |

Bivariate statistics for Bettonia chamberlaini (Elles) for the type locality sample.

Table 35

| $\quad$ Specimen | A | B | $\mathrm{B}_{3}$ | I | $\mathrm{R}_{1}$ | $Q$ |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
| SM Aroo84 | $6 \cdot \mathrm{I}$ | - | - | $\mathrm{II} \cdot 5$ | - | - |
| NMW 68.376.GI93 | $6 \cdot 2$ | - | - | $\mathrm{II} \cdot \mathrm{I}$ | - | - |
| NMW 68.376.GI94 | $3 \cdot 9$ | - | - | $8 \cdot 2$ | - | - |
| NMW 68.376.GI95 | - | $5 \cdot 5$ | $2 \cdot 2$ | $12 \cdot 9$ | - | - |
| NMW 68.376.Gr96 | - | $4 \cdot 3$ | $\mathrm{I} \cdot 8$ | - | - | - |
| BU 369 | $7 \cdot 5$ | $6 \cdot 0$ | $2 \cdot 5$ | - | - | - |
| BU 368 | - | - | - | - | $8 \cdot 0$ | $3 \cdot 3$ |
| NMW 68.376.GI97 | - | - | - | - | $6 \cdot 3$ | $2 \cdot 5$ |
| NMW 68.376.Grg8 | - | - | - | - | $5 \cdot 0$ | $2 \cdot 0$ |

Details of the length and width measurements for the cephalon and thorax, and for the position of the anterior pair of lateral glabellar furrows for Bettonia chamberlaini (Elles) from the type locality sample.

No data are available for the number of pygidial axial rings and pleural ribs above that given in the description above.

Discussion. See discussion of genus (page 158).

## Bettonia aff. superstes Whittard <br> (Pl. I4, fig. II)

Figured specimen. It. 2830 Internal mould of damaged cranidium with three thoracic segments.

Locality and horizon. Stream section at Wellfield Lodge immediately downstream of the point where the stream emerges after being piped under the road; shales assigned to $G$. teretiusculus Zone.

Description. A single specimen is known from the Llandeilo of the Builth district which shows affinity to Bettonia superstes. Although the fringe is damaged anteriorly three adventitious pits can be seen and assuming symmetrical distribution, it is calculated that about eight such pits would be present on the complete fringe; posterolaterally however no adventitious pits are developed. A prominent ridge separates the $E_{1}$ and $I_{1}$ arcs, whose pits are slightly larger than the rest, from the inner arcs. About twenty-eight pits are developed in the $\mathrm{E}_{1}$ arc on the right halffringe. Medially the arcs $\mathrm{I}_{1-3}$ are continuous, with $\mathrm{I}_{4}$ appearing at about row eight. Laterally the pits of the arcs $\mathrm{I}_{2-4}$ lose their radial arrangement due to the intercalation of auxiliary pits. The glabella and genal regions appear to be identical to those of other Bettonia and require no description.

The thoracic segments are not well preserved but appear to be of the normal trinucleid type. The pygidium is not known.

Discussion. The general features of this specimen are very similar to $B$. superstes. The fringe however differs in that there are no posterolateral adventitious pits, probably fewer anterior adventitious pits and slightly more pits in the $\mathrm{E}_{1}$ arc in the Builth specimen. However in view of the amount of variation now known to be present in Bettonia chamberlaini (Elles), it is considered undesirable to attempt a definite specific assignment until such time as details of the variation of $B$. superstes are known.

## Subfamily MARROLITHINAE Nov.

Diagnosis. See page $I 20$.

## Genus MARROLITHUS Bancroft, 1929

Diagnosis. See page i2I.
Type species. Trinucleus ornatus var. favus Salter, 1848.
Distribution. The genus is recorded with certainty only from the Anglo-Welsh region and the Armorican Massif. In the Armorican Massif it is represented by
M. bureaui (Oehlert, 1895), from the M. bureaui beds of the May syncline, possibly of Lower Llandeilo age (see Whittard, 1956: 54). M. bureaui has also been recorded from Portugal (Delgado, 1908: 58, 80) and Spain (Born, 1926: 202, 204). The occurrence of Marrolithus in the Builth district is of interest as it is the first record of the genus, albeit only as a rarity, from this part of the Anglo-Welsh area. The distribution now includes south-west Wales, and the Builth, Shelve, and Berwyn regions of the Anglo-Welsh faunal province; with M. ultimus Bancroft having been transferred to Costonia (Whittard, 1956: 50), the genus is no longer recognized from the South Shropshire outcrops east of the Longmynd.

## Marrolithus sp .

(Pl. 14, figs 6, 7)
Figured specimen. It. 278i Internal mould of cephalon.
Locality and Horizon. From the N. gracilis shales of the middle quarry, Llanfawr, Llandrindod.

Description. The solitary cephalon is an internal mould with the lower lamella. The cephalon is 12.3 mm wide medially and 4.9 mm long sagittally. The slightly convex anterior margin meets the concave lateral margins at about $90^{\circ}$ and forms protuberant anterolateral angles. The posterior margin is more or less straight. The glabella is clavate, encroaching slightly onto the fringe, shows slight traces of reticulation, and has one pair of very shallow pit-like lateral glabellar furrows situated posteriorly. The axial furrows are fairly wide, but there are no traces of alae. Anterior fossulae are present. The short occipital ring bears no trace of a spine. The straight, open posterior border furrows terminate in very shallow lateral pits. The genal regions are semi-elliptical, flatly convex and smooth; eye ridges and tubercles are absent. The base of the genal spines is inclined at about $45^{\circ}$ to the axial direction.

The fringe is poorly preserved anteriorly so that a precise fringe count cannot be made. The fringe terminates level with the posterior cephalic margin, with a short tongue extending behind the genal regions; it is narrowest anteromedially $(0.8 \mathrm{~mm})$ and widest (radially) at the anterolaterial corners $(3.0 \mathrm{~mm})$, located at about row 18. The following arcs and pits are developed:
$\mathrm{E}_{1}, \mathrm{I}_{1}$ continuous ( $\mathrm{E}_{1}$ with about 40 pits) ; $\mathrm{I}_{2}$ ?continuous; $\mathrm{I}_{3}, \mathrm{I}_{4}$ both commence slightly lateral to the axial furrows and continue to the genal angles; $\mathbf{I}_{5}$ has about eight pits and $\mathrm{I}_{6}$ about four pits, situated at the anterolateral corners.

The swollen areas consist of nine $\mathrm{I}_{1}$ pits (approximately row II-19), eight $\mathrm{I}_{2}$ pits (approximately row $12-19$ ) and four $\mathrm{I}_{3}$ pits (approximately row $15-18$ ). All the pits on the swollen area are enlarged as are the pits of $\mathrm{E}_{1}$ in rows $14-19$ (approximately) and $\mathrm{I}_{1}$ row 20. The increase in pit size along the anterior margin is gradual, but the decrease posteriorly along the lateral margin is more rapid. The girder is best
developed anteriorly, becoming less marked anterolaterally and laterally to reappear as a ventral ridge at the base of the genal spines.

The thorax and pygidium are unknown.
Discussion. The species seems to be most closely related to $M$. inornatus Whittard, 1956. The traces of reticulation on the internal mould suggests that the external surface of the exoskeleton may have been more strongly reticulated; this might distinguish the species from $M$. inornatus. The Builth specimen appears to differ in having a slightly larger swollen area, more markedly protuberant anterolateral corners, and also in that the glabella encroaches slightly onto the flange, though this latter feature may be as a result of compression. As the variation in these characters is unknown the importance of such slight differences cannot yet be assessed. Until more is known, it is preferred to leave this specimen unassigned specifically.

## Genus PROTOLLO YDOLITHUS Williams, 1948

Diagnosis. See page i2I.
Type species. Trinucleus ramsayi Hicks, 1875.
Distribution. The genus is known only from the Anglo-Welsh regions, being present in the Arenig of South Wales and Shelve and the Llandeilo of the Builth area.

Discussion. The genus is here considered as the most primitive member of the Marrolithinae. Lu and later Dean (1966: 281-283) showed that 'Trinucleus' primitivus Born, 1921, placed in Protolloydolithus by Whittard (1956), should be transferred to Hanchungolithus Lu, 1954, the genus is represented by only three species. The occurrence of Protolloydolithus reticulatus (Elles, 1940) at Builth is of interest because of its relatively high (Llandeilo) stratigraphic horizon; the other two species are confined to the Lower Llanvirn.

## Protolloydolithus reticulatus (Elles)

(Pl. 15, figs I, 5-9, II ; Pl. I6, fig. 2; Text-fig. I2)
1940 Trinucleoides reticulatus Elles: 427, pl. 29, figs 6-9.
1941 'Trinucleoides' veticulatus Elles; Lamont: 443.
1941 Trinucleoides reticulatus Elles; Whittington: 26.
1956 Protolloydolithus veticulatus (Elles); Whittard: 41.
Diagnosis. Protolloydolithus with between about forty and fifty pits in entire $\mathrm{E}_{1}$ arc; genal prolongations moderately developed; genae with fine reticulations and
caecae. Pygidium about three and a half times as wide as long, with between five and seven pleural ribs and up to sixteen axial rings.

Type material. Holotype. BM I 7216 (Pl. 15, fig. 1) Internal mould of almost complete specimen.

Paratypes. BM I 7328 (Pl. 15, fig. II) Internal and external moulds of damaged cephalon. It. 8604 (Pl. 15, fig. 7) Internal and external moulds of nearly complete thorax and pygidium.

Dimensions.

|  | B | $\mathrm{I}_{1}$ | Q | $\mathrm{Q}_{1}$ | $\mathrm{R}_{1}$ |
| :--- | :---: | :---: | :---: | :---: | :---: |
| Holotype | c. $6 \cdot 5$ | c. $15 \cdot 0$ | $4 \cdot 5$ | $0 \cdot 9$ | $\mathrm{I}_{3} \cdot \mathrm{O}$ |
| I 7328 | c. $6 \cdot 0$ | c. $\mathrm{I} 5 \cdot 0$ | - | - | - |


|  |  |  |  | No. of | No. of ribs |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
|  | W | X | Z | axial rings | Left | Right |
| Holotype | c. I2.O | c. I•8 | 3.5 | II+ | 6 | - |
| It. 8604 | c. II.O | c. I. 8 | c. $3 \cdot 5$ | - | 6 | - |

All measurements in mm . For explanation of symbols see Text-fig. I.

Type locality and horizon. It is almost certain that the holotype and the paratypes come from the stream section in shales of Llandeilo age to the east of Bach-y-graig, Llandrindod. The label accompanying the holotype gives the locality as 'Cym-y-rhain Dingle on stream behind Pump House, Llandrindod Wells, Radnorshire'. Labels with the paratypes give the locality variously as 'Stream E. of Hillside' and 'Llandrindod Wells'. All new specimens collected are from the left bank of the stream section east of Bach-y-graig 65 yds east of the point where the footpath enters the wood at the western end of the section.

Other figured material. It. 2782 (Pl. 15, fig. 6; Pl. 16, fig. 2) ; It. 2783 (Pl. 15, fig. 8) ; It. 2784 (Pl. 15, fig. 5) ; NMW 15.207.G3 (Pl. 15, fig. 9).

Distribution. The species is not known outside the type locality.
Description. Excluding the genal prolongations and spines, complete specimens are subcircular, with a semicircular cephalon.

The moderately convex glabella possesses a pseudofrontal lobe which extends for two-thirds of the glabellar length. The glabella is traversed anteriorly by a weakly developed furrow delimiting a small triangular preglabellar field that encroaches a short distance onto the fringe. Three pairs of pit-like lateral glabellar furrows are developed on the sides of the glabella. The anterior pair, which are the smallest, are situated at about two-fifths the distance along the glabella from the anterior. The median and posterior pairs are somewhat larger and deeper and occur at about two-thirds and four-fifths of the glabellar length respectively. Alae extend posteriorly from just behind the anterior pair of lateral glabellar furrows. Lateral, and subparallel to the posterior part of each ala a low elongate swelling of uncertain
significance is present in the floor of the axial furrows, which are wide at the posterior. The presence of this swelling in several specimens suggests it to be an original feature of the exoskeleton, and not due to any post mortem distortion. Medially, the external surface of the glabella is pitted, with a low median glabellar node near the front.

The occipital ring is short (sag.) slightly convex posteriorly, and bears no occipital spine. The occipital furrow is extremely shallow medially, deepening laterally to form shallow occipital pits.
Anteriorly the axial furrows follow the lateral margins of the pseudofrontal lobe until opposite the anterior pair of lateral glabellar furrows; posteriorly from this point the straight furrows become wider and shallower. Poorly developed pits mark the site of the anterior fossulae.

Internally the lateral glabellar furrows form small raised platforms.
The genal regions are quadrant-shaped, with the inner margin slightly concave. The genae are only slightly convex, but with a moderately steeply declined outer margin. The exterior surface is covered with a fine reticulate pattern of raised ridges distributed over the genae in the normal trinucleid manner. Two fine genal caecae, originating approximately level with the anterior of the alae also cross this area posteriorly. The presence of only one caeca in some specimens is considered to be a reflection of imperfect preservation.

The posterior border is sharply upturned behind the straight, shallow, though clearly developed posterior border furrow. It is highest at the fulcrum where it


Fig. 12. Reconstruction of the cephalon of Protolloydolithus reticulatus (Elles) in dorsal view. c. $\times 5$.
turns abruptly posterolaterally. The crest of the border appears to bear a few parallel terrace lines.

Observations on the poorly preserved fringe show that an orderly $E_{1}$ arc is developed together with several internal arcs; of the latter only $I_{1}$ arc is orderly arranged. The $\mathrm{E}_{1}$ arc has between nineteen and twenty-six pits developed on each half-fringe and is separated from the $I_{1}$ arc on the upper lamella by a sharp, high ridge with the $I_{1}$ pits situated on its inner slope. At least five irregularly arranged $I$ arcs internal to $I_{1}$ are present anteriorly and show some tendency to radial arrangement medially. Laterally the number of pits increases and the distribution becomes entirely haphazard. The pits of these inner arcs are smaller than those of the $\mathrm{E}_{1}$ and $\mathbf{I}_{1}$ arcs. Moderately large genal prolongations are developed and about seven or eight pits of the $\mathrm{E}_{1}$ arc lie behind the posterior margin of the cephalon. The pitted area extends medially as far as the fulcrum. Little is known of the lower lamella but there is no reason to suspect any discordance between the pits of the two lamellae. The strongly developed girder merges posteriorly into the genal spines.

Although the genal spines are not preserved in their entirety they probably extend some way behind the pygidium.

The suture is not seen, but it seems most likely that the suture is marginal, becoming dorsal at the genal angles as in other trinucleids.

As pointed out by Lamont (194I: 443) and Whittard (1956:4I), the thorax has only six segments and not seven as recorded by Elles (1940: 427). In outline it is rectangular, about three times as wide as long, the convex (tr.) axial rings contrasting with the flat pleural regions. The articulating furrows are narrow and deeper laterally than medially. The pleurae are crossed by a shallow oblique pleural furrow which extends into the posteriorly deflected, blunt terminations. The fulcral processes on the anterior edge are proportionately nearer the axial furrows than in most other trinculeid genera.

The roundly triangular pygidium is about three and a half times as wide as long. The axis tapers gently and has at least sixteen axial rings developed which are poorly defined posteriorly. The tubercles mentioned by Whittard (1956:4I) on the axial rings have not been observed. The pleural fields have a narrow (sag.) anterior border and a triangular terminal area together with six, or less commonly five or seven, ribs. These widen distally to become progressively more posteriorly directed. The strongly declined posterolateral border bears terrace lines. Although relatively few data are available, there appears to be no correlation between the size of the pygidium and the number of ribs (see Table 38). No examples of the asymmetrical development of the ribs on the two halves of the pygidium are known.

Ontogeny. A single poorly preserved specimen most probably represents a meraspis degree three or four (Pl. 15, fig. 8). It appears similar to the holaspid form apart from the number of thoracic segments and overall size. A further small cephalon (width approximately 5.0 mm ) probably referable to this species, shows a slightly carinate glabella.

Biometrical data. Because of poor preservation very few data are available for this species; such data as are available are given in Tables $36-38$ below.

Table 36

| Spec. No. | A | $\mathrm{A}_{1}$ | B | $\mathrm{~B}_{1}$ | $\mathrm{~B}_{2}$ | $\mathrm{~B}_{3}$ | I | $\mathrm{I}_{1}$ | K | $\mathrm{~K}_{1}$ |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| It. 2783 | - | c. $\mathrm{I} \cdot 2$ | - | - | - | $-c$. | 3.5 | - | - | - |
| It. 2784 | - | $-c .3 .8$ | - | - | - | $-c .8 .5$ | - | - |  |  |
| NMW I5.207.G3 | - | - | 6.0 | 5.0 | 4.2 | - | 17.4 | 13.2 | 3.5 | - |
| It. 8809 | - | - | 5.4 | 4.2 | 3.4 | - | $-c .12 .0$ | - | - |  |
| NMW 68.376.G200 | 6.9 | 7.3 | 5.7 | 4.5 | 3.5 | 2.3 | - | - | 4.2 | $\mathrm{I} \cdot 8$ |
| It. 8807 | 6.4 | - | 4.9 | - | - | - | - | 10.5 | 3.0 | - |

Details of measurements made on Protolloydolithus veticulatus (Elles). All measurements in mm . For explanation of symbols see Text-fig. I.

## Table 37

| x : y | $\overline{\mathrm{x}}$ | var. x | $\overline{\mathrm{y}}$ | var. y | r | $\mathrm{r}_{\mathrm{e}}$ | $\alpha$ | var. $\alpha$ | a | var. a | n |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| W: Z | 9.66 | 3.7862 | 2.79 | 0.3114 | 0.937 | 0.938 | 0.99 | 0.0236 | 0.29 | 0.00200 | 7 |
| W: X | 9.66 | 3.7862 | 1.39 | 0.1214 | 0.936 | 0.937 | 1.24 | 0.0373 | 0.18 | 0.00080 | 7 |
| X: Z | 1.39 | 0.1214 | 2.79 | 0.3114 | 0.924 | 0.927 | 0.80 | 0.0181 | 1.60 | 0.07463 | 7 |

Bivariate statistics for the pygidium of Protolloydolithus veticulatus (Elles). All measurements in mm . For explanation of symbols see Text-fig. I.

Table 38

|  |  | No. of pleural ribs |  |
| :---: | :---: | :---: | :---: |
| Spec. No. | Pygidial length | Left | Right |
| NMW 68.376.G20I | I. 8 | 7 | 7 |
| It. 2784 | $2 \cdot 2$ | 5 | 5 |
| NMW 68.376.G202 | $2 \cdot 2$ | 7 | 7 |
| It. 8806 | $2 \cdot 2$ | 7 | 7 |
| NMW 68.376.G203 | $2 \cdot 6$ | - | 6 |
| NMW 68.376.G204 | $3 \cdot 0$ | 6 | 6 |
| NMW 68.376.G200 | $3 \cdot 3$ | 6 | 6 |
| It. 8808 | $3 \cdot 3$ | 6 | 6 |
| NMW 15.207.G3 | $3 \cdot 3$ | 6 | 6 |

Table showing the lack of correlation between the number of pleural ribs developed and pygidial length in Protolloydolithus veticulatus (Elles).

Discussion. Elles's original placing of this species in the genus Trinucleoides Raymond, I9I7 cannot be upheld, for whilst the well-developed alae of $P$. reticulatus bear some resemblance to the lateral lobes of Trinuceoides reussi (Barrande, 1872), the structure of the fringe in the two species is completely different.

Protolloydolithus ramsayi (Hicks, 1875) is similar to P. reticulatus but may be distinguished by its smaller genal prolongations, less well developed alae, probable
higher number (six-eight) of arcs internal to $\mathrm{I}_{1}$ and its relatively wider pygidium. The only other species referred to the genus, $P$. neintianus Whittard, 1956, is readily separated on the narrowness of the fringe anteriorly and the unfurrowed pleural fields of the pygidium.

Morphologically the species shows no new features apart from the possible development of terrace lines along the crest of the posterior cephalic border which is a structure apparently previously unrecognized in the trinucleids.

## Genus TELAEOMARROLITHUS Williams, 1948

Diagnosis. See page I2I.
Type species. Trinucleus radiatus Murchison, 1839.
Distribution. The genus is restricted to the basal Caradoc (N. gracilis Zone) of the Anglo-Welsh faunal province, being represented in the Llandeilo, Builth and Shelve regions.

Discussion. Williams (1948: 85) considered Telacomarrolithus to have been derived from the marrolithids by the collapse of the swollen area. The occurrence at Builth of $T$. intermedius sp. nov. with a slightly swollen area ventrally and expanded pits in the $\mathrm{E}_{1}$ arc of the lower lamella gives support to Williams' belief that Telaeomarrolithus is more closely related to the marrolithids than to Trinucleus. However, the presence of expanded pits solely in the $\mathrm{E}_{1}$ arc, a feature not found in any other marrolithinid, suggests that it may not be derived directly from Marrolithus favus (Salter, 1848) as suggested by Williams, or indeed from any marrolithinid known at present.

Telaeomarrolithus intermedius sp. nov.
(Pl. 15, figs 2-4, IO; Pl. I6, figs I, 4-9; Text-fig. I3)
Diagnosis. Telaeomarrolithus with about thirty-eight to forty-four pits in $\mathrm{E}_{1}$ arc, of which five or six at anterolateral corners are markedly expanded on the lower lamella; occasional pits external to the girder but internal of $\mathrm{E}_{1}$ developed anterolaterally; maximum of about seven pits in anterolateral rows; four in median rows.

Type material. Holotype. It. 2785 (Pl. 16, figs I, 5) Internal and external moulds of cephalon.

Paratypes. It. 2789 (Pl. ェ6, fig. 4) Internal mould of cephalon. It. 2788 (Pl. 16, fig. 8) Internal and external moulds of possibly enrolled specimen showing part of thorax. It. 2786 (Pl. 16, fig. 6) Internal mould of small cranidium. It. 2787 (Pl. 16, fig. 9) Internal mould of damaged cranidium. It. 8606 (Pl. 15, fig. 4) Mould of lower lamella. It. 8799 (Pl. 15, fig. 2) Internal mould of damaged cranidium. It. 8800 (Pl. 15, fig. 3) External mould of cephalon. BM In. 48533 (Pl. 15, fig. Io) Internal mould of cranidium. USNM 160108 (Pl. 16, fig. 7) External mould of disarticulated entire specimen.

Dimensions.

|  |  | A | $\mathrm{A}_{1}$ | B | $\mathrm{~B}_{1}$ | $\mathrm{~B}_{2}$ | $\mathrm{~B}_{3}$ |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| $\mathrm{~B}_{4}$ |  |  |  |  |  |  |  |
| It. 2785 | $8 \cdot 5$ | $9 \cdot \mathrm{I}$ | $6 \cdot 7$ | $5 \cdot 2$ | $4 \cdot \mathrm{I}$ | c. $2 \cdot 7$ | $2 \cdot 9$ |
| It. 2786 | $3 \cdot 8$ | $4 \cdot \mathrm{I}$ | $2 \cdot 9$ | - | - | - | - |
| It. 2787 | $6 \cdot 4$ | $6 \cdot 7$ | $4 \cdot 8$ | $3 \cdot 9$ | $3 \cdot 0$ | $2 \cdot \mathrm{I}$ | - |
| It. 2789 | - | - | $6 \cdot 6$ | $5 \cdot 4$ | $4 \cdot 2$ | $3 \cdot 0$ | - |
| It. 2790 | c. $9 \cdot \mathrm{I}$ | c. $9 \cdot 6$ | c. $7 \cdot 0$ | - | $4 \cdot 5$ | $3 \cdot \mathrm{I}$ | - |
| In. 48533 | $7 \cdot 8$ | $8 \cdot 2$ | $5 \cdot 9$ | $4 \cdot 3$ | $3 \cdot 6$ | $2 \cdot 5$ | - |


|  | I | $\mathrm{I}_{1}$ | K | $\mathrm{~K}_{1}$ |
| :--- | :---: | :---: | :--- | :---: |
| It. 2785 | - | c. 13.5 | 4.5 | 3.0 |
| It. 2786 | - | $6 \cdot 9$ | $2 \cdot \mathrm{I}$ | $\mathrm{I} \cdot \mathrm{O}$ |
| It. 2787 | - | - | 3.3 | $\mathrm{I} \cdot 8$ |
| It. 2789 | c. I 7.5 | - | - | - |
| It. 2790 | - | - | 4.7 | - |
| In. 48533 | I 7.3 | I 3.2 | 4.0 | $\mathrm{I} \cdot 9$ |

All measurements in mm. For explanation of symbols see Text-fig. I.

Fringe Data

|  | Number of pits <br> in $E_{1}$ arc |  | Number of expanded <br> pits in $E_{1}$ arc |  | Presence of <br> Left |
| :--- | :---: | :---: | :---: | :---: | :---: |
| Right | Left | Right | Row O |  |  |
| It. 2785 | I9 $\frac{1}{2}$ | I9 $\frac{1}{2}$ | - | - | present |
| It. 2789 | - | c. 20 | - | - | ? |
| It. 2790 | - | I9 | - | 5 | $?$ |
| In. 48533 | $20 \frac{1}{2}$ | $2 I_{\frac{1}{2}}$ | 6 | 5 | present |


|  | Max. Number of I arcs |  | Number of I arcs medially |  | Position of anterolateral angulation |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Left | Right | Left | Right | Left | Right |
| It. 2785 | - | - | - | - | row 12 | row II |
| It. 2788 | - | ?6 | - | - | - | - |
| It. 2789 | - | ?6 | - | 4 | - | c. row 12 |
| It. 2790 | - | ?6 | - | ? 3 | - | row II-12 |
| In. 48533 | - | ? 5 | 4 | 4 | row 12 | row 13 |

Type locality and horizon. N. gracilis shales exposed in the middle quarry, Llanfawr, Llandrindod.

Distribution. The species is known only from the type locality.
Description. The cephalon is about twice as wide as long, excluding the genal
spines. The lateral margins are straight and slightly divergent anteriorly; anterior margin arched forwards medially; anterolateral corners angulate.

The glabella is convex, with the pseudofrontal lobe occupying the anterior threefifths; it is of moderately convex profile anteriorly and gives the impression of encroaching onto the fringe in compressed specimens. The poorly preserved anterior lateral glabellar furrows are weakly developed. The median pair, delimiting the posterior of the pseudofrontal lobe, are better developed and consist of elongate (tr.), rather shallow pits. The posterior pair are again elongate pits, but are directed slightly anteromedially. A small median glabellar node is situated about half-way along the glabella. A coarse reticulate pattern is developed medially on the glabella. Alae extend posteriorly from the rear of the pseudofrontal lobe. A weakly developed occiput is present.

The occipital ring is short (sag.) consisting of little more than a median continuation of the low ridge forming the posterior margin of the genal regions. The occipital furrow is shallow; no occipital spine is developed.

The shallow axial furrows are most clearly defined anteriorly where a pair of anterior fossulae are developed.

The genal regions are quadrant-shaped and apart from the steeply declined outer margin are only slightly convex. Traces of a course reticulation are present distributed in the typical trinucleid manner. In some specimens a small lateral eye tubercle appears to be developed on each gena, close to the axial furrows and slightly anterior of the median lateral glabellar furrows, although eye ridges are lacking (Pl. I6, fig. 4). The posterior margin is upturned to form a low ridge-like border


Fig. 13. Reconstruction of the cephalon of Telaeomarrolithus intermedius sp. nov. in dorsal view. c. $\times 5$.
separated from the genae by a straight, shallow posterior border furrow which terminates in a small lateral pit.

Internally the lateral glabellar furrows form raised platforms; the anterior fossulae and the lateral pits having corresponding apodemes. Internal traces of the reticulation on the median glabellar node are only rarely seen (Pl. i6, fig. I).

The upper lamella of the fringe is widest anterolaterally, and narrowest medially. Between about nineteen and twenty-two radial rows are present on each half-fringe. The pits of the $E_{1}$ and $I_{1}$ arcs are larger than those of the other $I$ arcs, and anterolaterally the pits of $E_{1}$ tend to be slightly enlarged. A few specimens show pits of two E arcs developed in up to four radial rows at the anterolateral corners (Pl. I5, figs 2, 10). Traces of such pits have only been detected on one lower lamella in which they appear to be developed internal to $\mathrm{E}_{1}$ on the outer steep sides of the swolled area. The significance of these pits, and their apparent absence in some specimens is not known. Arcs $\mathrm{I}_{1-3}$ appear to be present medially, $\mathrm{I}_{4}$ appearing in row two or three. At least six I arcs are developed anterolaterally. The radial arrangement of the pits only breaks up at the genal angles where moderate genal prolongations are developed with three or four pits of the $\mathrm{E}_{1}$ and $\mathrm{I}_{1}$ arcs located behind the posterior margin of the genal regions. Laterally the fringe is differentiated into two regions, the outer being characterized by more strongly developed ridges between the radial rows. Only the pits of the $E_{1}$ and $I_{1}$ arcs lie in the outer zone, the arcs becoming more widely separated at the anterolateral corners.

The inner part of the lower lamella is steeply declined to the very strongly developed, smooth girder; the outer part being reflected sharply dorsally from the girder. The pit distribution corresponds to that of the upper lamella, but in addition four or five pits in the $E_{1}$ arc are generally markedly expanded at the anterolateral corners which occurs at about row twelve. In addition low, weakly developed ridges are present laterally between the various I arcs. From the material available it appears that either a row of pits or a ridge may lie along the sagittal line.

The girder merges posterolaterally with the long, slightly divergent genal spines. On one paratype (It. 2789 ) of cephalic width approximately 17.5 mm , the genal spines are about 14.5 mm long.

The course of the suture is not seen, but is presumably marginal, becoming dorsal only at the genal angles and may be non-functional (see discussion).

The thorax is typically trinucleid and requires no further description.
The sole known pygidium (Pl. 16, fig. 7) is triangular in outline being about three and a half times as wide as long. Its overall morphology is extremely similar to that of the pygidium of Trinucleus fimbriatus and isolated pygidia cannot be distinguished. At least five pleural ribs and six axial rings are developed. The steeply declined posterior border bears terrace lines on the external surface.

Biometrical data. In view of the small number of measurements possible, full details are given. In addition to those already given for the type of specimens, further measurements are given in Table 39. Since very few exact pit counts could be made, no further statistical data can be given for the pit distribution on the fringe above that given in the description.

Table 39

| $\quad$ Spec. No. | A | $\mathrm{A}_{1}$ | B | $\mathrm{~B}_{1}$ | $\mathrm{~B}_{2}$ | $\mathrm{~B}_{3}$ | $\mathrm{~B}_{4}$ | $\mathrm{I}_{1}$ | K | $\mathrm{~K}_{1}$ |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| NMW 68.376.G205 | 5.9 | 6.2 | 4.2 | 3.2 | 2.5 | - | - | 8.5 | 2.8 | $\mathrm{I} \cdot 3$ |
| NMW 68.376.G206 | - | $7 . \mathrm{I}$ | - | - | - | - | - | - | - | - |
| NMW 68.376.G207 | - | - | 5.5 | 4.3 | 3.5 | - | - | 12.5 | 3.4 | $\mathrm{I} \cdot 9$ |
| It. 279I | 8.5 | 8.9 | 6.4 | - | - | - | 3.5 | I 2.7 | - | 2.4 |
| It. 8605 | 5.0 | 5.3 | 3.8 | - | - | - | - | 8.5 | - | - |

Details of measurements made on the cephalon of Telaeomarrolithus intermedius sp. nov. in addition to those made on the type material. All measurements in mm. For explanation of symbols see Text-fig. 1 .

Discussion. Only thirty specimens of this new species are known from the middle quarry, Lanfawr and it is thus relatively rare compared with the majority of species at that locality.

The morphological features developed in this species make generic placing a little difficult. Dorsally the cephalic exoskeleton shows strong similarities to Trinucleus fimbriatus with its well developed radial sulci and anteriorly swollen glabella. However the presence of two distinct areas on the fringe laterally, the angulate outline and the presence of markedly swollen pits in the $\mathrm{E}_{1}$ arc on the lower lamella are thought to indicate that the species is best placed in Telaeomarrolithus. The new species is easily distinguished from the type species by its expanded pits on the lower lamella, the presence of two pits external to the girder in the anterolateral rows, the smaller number of pits in each arc, and the smaller number of $I$ arcs represented anterolaterally. Telaeomarrolithus sp. indet. described by Whittard (1956: pl. 9, fig. 6) is too poorly preserved for any proper comparison, although the rather rounded anterolateral angles are more like those of $T$. vadiatus than that of $T$. intermedius.

About two-thirds of the internal moulds of $T$. intermedius have the impression of the ventral surface of the lower lamella preserved, indicating that the lower lamella was still attached to the cephalic exoskeleton. This type of preservation is only rarely found in specimens of Trinucleus fimbriatus from the same locality. In view of this, and that the trilobite exoskeletons are generally disarticulated, it seems possible that the marginal suture of $T$. intermedius was no longer functional. It is interesting to note that the four specimens of T. radiatus referred to by Williams (1948: 83) together with a further specimen from Llandeilo all show the same mode of preservation and it may be that an ankylosed marginal suture is characteristic of Telaeomarrolithus.

## Telaeomarrolithus radiatus (Murchison)

> (Pl. I6, fig. 3)

1839 Trinucleus vadiatus Murchison 66o, pl. 23, figs 3a, 3b.
1948 Telaeomarrolithus vadiatus (Murchison); Williams: 83, text-fig. i1, pl. 6, fig. 10.
Type material. Syntypes. GSM Geol. Soc. Coll. 6836; GSM Geol. Soc. Coll. 6837.

Discussion. Murchison's localities for Trinucleus radiatus read, 'Trilobite Dingle, Welsh Pool, Caradoc and Meifod Hills etc.', (Murchison, $1839: 660$ ), but there is some doubt as to the locality of the figured syntypes, for the original label gives the locality as 'Llandeilo Flags, Builth'. However the lithology of the syntypes does not match anything known from the Builth region, but is similar to that of Williams's specimens from Crûg, near Llandeilo. It thus seems more probable that the types come from the Llandeilo, rather than the Builth area. This is supported by the fact that no other specimens of $T$. radiatus are known from the Builth region and it is thus proposed to remove T. radiatus from the faunal lists of the region.

## IV. ACKNOWLEDGEMENTS

The bulk of the material used for this study was collected during the tenure, at the Queen's University of Belfast, of a research studentship awarded by the Natural Environment Research Council to whom I am grateful for financial assistance. All new type and figured material is deposited in the collections of the British Museum (Natural History), London, together with some further specimens. I am much indebted to Professor Alwyn Williams and Dr A. D. Wright for their supervision and encouragement whilst the work was in progress. My thanks are also given to Professor H. B. Whittington for much helpful advise and discussion in the later stages of the work, to Dr D. L. Bruton for kindly reading the manuscript, and to Mr John Lewis for his skill in drawing all the Text-figures. I am also indebted to Sir William Pugh and the late Professor O. T. Jones for generously supplying information concerning fossiliferous localities.

I thank Dr D. A. Bassett, National Museum of Wales, Cardiff; Mr A. G. Brighton and Dr C. L. Forbes, Sedgwick Museum, Cambridge; Dr F. H. Broadhurst, University of Manchester ; Dr W. T. Dean, formerly at The British Museum (Nat. Hist.); Dr P. M. Kier, United States National Museum, Washington, D.C.; Mr C. W. Newman, Radnorshire County Museum, Llandrindod Wells; Mr H. P. Powell, University of Oxford; Dr A. W. A. Rushton, Institute of Geological Sciences; Dr I. Strachan, University of Birmingham and Mr J. T. Wattison, Stoke-on-Trent, for the loan of specimens in their care.

## V. REFERENCES

Angelin, N. P. 1854. Palaeontologia Scandinavica. Fase. II. ix $+21-92,42$ pls. Lund. Bancroft, B. B. 1929. Some new species of Cryptotithus (s. l.) from the Upper Ordovician Mem. Proc. Manchr. lit. phil. Soc., Manchester 73: 67-98, pls I-2.
Barrande, J. 1852. Systême silurien du centre de la Bohême. i ève partie. Récherches paléontologiques. $\mathrm{xxx}+935 \mathrm{pp}$. . Atlas of 51 plates. Prague and Paris.
-_1872. Systême silurien du centre de la Bohême. I ève partie. Récherches paléontologiques, I (supplement). $\quad \mathbf{x x x}+647$ pp., Atlas of 35 plates. Prague and Paris.
Bates, D. E. B. Ig68. The Lower Palaeozoic Brachiopod and Trilobite Faunas of Anglesey. Bull. Br. Mus. nat. Hist., (Geol.), London 16 (4): 125-199, 14 pls, 2 text-figs.

Boeck, C. P. B. 1838 Gaea Norvegia 1: 138-145. Christiania.
Born, A. 1921. Eine Untersilurfauna aus den Montagnes noires (Centralplateau). Senckenbergiana, Frankfurt a.m. 3: $18 \mathrm{r}-193$, 1 fig.
1926. Palaeontologisch-stratigraphischer Beitrag to Beitrag zur Geologie der Sierra Morena nördlich von la Caraolina (Jaen) by W. Henke. Abh. senckenb. naturforsch. Ges., Frankfurt 39: 201-204
Dean, W. T. 1966. The Lower Ordovician Stratigraphy and Trilobites of the Landeyran Valley and the neighbouring district of the Montagne Noire, south-western France. Bull. Br. Mus. nat. Hist., (Geol.), London 12 (6): 245-353, pls $1-2$ r.

- 1967. The Correlation and Trilobite Fauna of the Bedinan Formation (Ordovician) in south-eastern Turkey. Butl. Br. Mus. nat. Hist., (Geol.), London 15 (2): 81-123, pls 1-10, 4 text-figs.
Delgado, J. F. N. 1908. Système silurique du Portugal. Étude de stratigraphie paléontologique. Mém. Commn. geol. Port., Lisboa. I-245, pls I-8.
Elles, G. L. 1940. The Stratigraphy and Faunal Succession in the Ordovician rocks of the Builth-Llandrindod Inlier, Radnorshire. O. Jl geol. Soc. Lond. 95: 383-445, pls 27-32.
Fisher, D. W. 1962. Correlation of the Ordovician Rocks in New York State. New York State Museum and Sci. Service Geol. Surv. Map and Chavt Ser. No. 3 Albany.
Foerste, A. F. 1910. Preliminary notes on Cincinnation and Lexington fossils of Ohio, Indiana, Kentucky and Tennessee. Bull. Scient. Labs. Denison Univ., Granville, Ohio 16: $15-87$, pls $\mathrm{I}-6$.
Green, J. 1832. A monograph of the trilobites of North A merica: with coloured models of the species. 94 pp ., io figs. Philadelphia.
Hawle, I. \& Corda, A. J. C. 1847. Prodrom einer Monographie der böhmischen Trilobiten. 176 pp., 7 pls. Prague.
Hicks, H. 1875. On the Succession of the ancient rocks in the vicinity of St David's, Pembrokeshire, with special reference to those of Arenig and Llandeilo groups, with their fossil contents. O. Jl geol. Soc. Lond. 31: 167-195, pls 8-1 I.
Hisinger, W. 1840. Lethaea Svecia seu Petrificata Sveciae iconibus et characteribus illustrata. Supplementum secundum. Holmiae.
Hughes, C. P. 1969. The Ordovician Trilobite Faunas of the Builth-Llandrindod Inlier, Central Wales. Part I. Bull. Br. Muts. nat. Hist., (Geol.), London 18 (3): 39-103, 14 pls, 6 text-figs.
- 1970. Statistical Analysis and Presentation of Trinucleid (trilobita) Fringe data. Palaeontology, London 13 (r) : i-9.
Hughes, C. P. \& Wright, A. J. 1970. The Trilobites Incaia Whittard, 1955 and Anebolithus gen. nov. Palaeontology, London 13 (4): 677-690, pls 127, 128.
Klouček, C. 1916. Ovrstvách $\mathrm{d}_{1}{ }_{\gamma}$, jich trilobitech a nalezištích. Rozpr. české Akad. Véd Uméni, Prague 25 (39) : 1-21.
Lamont, A. 1941. Trincucleidae in Eire. Ann. Mag. nat. Hist., London (if) 8: 438-469, pl. 5 .
- 1948. Indications of cephalic sutures in Trinucleidae and Harpididae. Nature, London 162: 376-377.
Link, D. H. F. 1807. Beschreibung der Naturalien-Sammlung der Universität zu Bostock. Abth. 4.
Lu, Y. H. 1954. A brief note on the Upper Ordovician trilobites from Tangshan, Nanking. Proc. Pal. Soc. China, Nanking 7 :
M'Coy, F. 1849. On the classification of some British fossil Crustacea with notices of some new forms in the University collection at Cambridge. Ann. Mag. Nat. Hist., London (2) 4: 161-179, 330-335, 392-414.

Moore, R. C. 1959. Treatise on Invertebrate Paleontology. Part O. Avthropoda I. xix + 560 pp., 415 figs. Lawrence \& Meriden.

Murchison, R. I. 1839. The Silurian System founded on geological researches in the counties of Salop, Hereford, Radnor, Montgomery, Caermarthen, Brecon, Pembroke, Monmouth, Gloucester, Worcester and Stafford; with descriptions of the coal-fields and overlying formations xxxii +768 pp ., 40 pls. London.
—— 1859. Siluria. 3rd edit. xix +592 pp., 41 pls. London.
Oehlert, D. P. 1895. Sur les Trinucleus de l'ouest de la France. Bull. Soc. géol. Fr., Paris (3) 23: 299-336, pls I, 2.

Přibyl, A. \& Vaněk, J. 1969. Trilobites of the family Trinucleidae Hawle et Corda, 1847 from the Ordovician of Bohemia. Sb. geol. Ved., Prague (P) 11: 85-137, pls i-16.
Raymond, P.E. 1913. Some changes in the names of genera of Trilobites. Ottara Naturalist 26: $1-6$.
1913a. A further note on Cryptolithus versus Trinucleus. Ottawa Naturalist 27: 26-30. 1917. Beecher's classification of the trilobites after twenty years. Am. J. Sci., New Haven (4) 43: 196-2 10.
1925. Some trilobites of the Lower Middle Ordovician of eastern North America. Bull. Mus. comp. Zool. Havv., Cambridge 67: i-r8o, pls i-10.
Reed, F. R. C. 1895. New Trilobites from the Bala beds of County Waterford. Geol. Mag., Lond. (4) 2: 49-55.
1912. Notes on the genus Trinucleus. Geol. Mag., Lond. (5) 9:346-353, 385-394, pls 18, 19. 1914. Notes on the genus Trinucleus. Geol. Mag., Lond. (6) 1:349-359, pls 28, 29.

Salter, J. W. 1848. In Phillips, J. \& Salter, J. W. Palaeontological appendix to Professor John Phillips' Memoir on the Malvern Hills, compared with the palaeozoic districts of Abberley, etc. Mem. Geol. Suvv. U.K., London 2: 331-386, pls 4-30.
1853. Figures and descriptions illustrative of British organic remains. Mem. geol. Surv. U.K., London 7: 1-8, pl. 7.
1866. A monograph of the British Trilobites of the Cambrian, Silurian and Devonian Formations. Part III. Palaeontogy. Soc. [Monogr.], London. 129-r76, pls 15-25
Sedgwick, A. \& M'Coy, F. 1851-1855. A synopsis of the classification of the British Palaeozoic rocks, with a systematic description of the British Palaeozoic fossils in the geological museum of the University of Cambridge. i-iv, $\mathrm{I}-\mathrm{I} 84$, Ir pls, 185 I ; $\mathrm{i}-\mathrm{x}, \mathrm{r} 85-406, \mathrm{pl}$ IH, I, K, L. $2 \mathrm{~A}, \mathrm{~B}, 1852$; i-xcviii, $407-662$, pls $2 \mathrm{C}, \mathrm{D}, 3 \mathrm{~A}-\mathrm{I}, \mathrm{K}, 1855$. London and Cambridge.
Shaw, A. B. 1957. Quantitative trilobite studies II. Measurements of the dorsal shell of non-agnostidean trilobites. J. Paleont., Tulsa 31: 193-207.
Shaw, A. B. \& Stubblefield, C. J. 1950. Tvinucleus Murchison, 1839 as a nomen conservandum. J. Paleont., Tulsa 24: 624-625.
Stetson, H. C. 1927. The distribution and relationships of the Trinucleidae. Bull. Mus. comp. Zool., Havv., Cambridge 68: 87-104, I pl.
Størmer, L. 1930. Scandinavian Trinucleidae, with special reference to Norwegian species and varieties. Skr. Norsk Vidensk.-Akad. Mat. Naturv. Kl., Oslo 1 (4): i-Iri, pls 1-14.
Stubblefield, C. J. \& Whittington, H. B. 1956. Proposed use of plenary powers to validate the generic names Trinucleus Murchison, 1839, and Tretaspis M'Coy, 1849 (Class Trilobita). Bull. zool. Nomencl., London 12: 49-54.
Vogdes, A. W. 1890. A bibliography of Palaeozoic Crustacea from 1698 to 1889 including a list of North American species and a systematic arrangement of genera. Bull. U.S. geol. Surv., Washington 63 : r-r 77.
Whittard, W. F. 1955-67. The Ordovician trilobites of the Shelve Inlier, West Shropshire. Palaeontogr. Soc. [Monogr.], London: 1-40, pls 1-4, 1955; 41-70, pls 5-9, 1956; 7 1-116, pls 10-15, 1958; 117-162, pls 16-21, 1960; 163-196, pls 22-25, 1961; 197-228, pls 26-33, 1961a; 229-264, pls 34-45, 1964; 265-306, pls 46-59, 1966; 307-352, 1967.
Whittington, H. B. i940. On some Trinucleidae described by Joachim Barrande. Am.J. Sci., New Haven 238: $24^{1-259}$, pls 1-4.
194r. The Trinucleidae-with special reference to North American genera and species. J. Paleont., Tulsa 15: 21-41, pls 5, 6.

Whittington, H. B. x94ıa. Silicified Trenton Trilobites. J. Paleont., Tulsa 15: 492-522, pls $72-75$.
1959. Silicified Middle Ordovician trilobites: Remopleuridae, Trinucleidae, Raphiophoridae, Endymionidae. Bull. Mus. Comp. Zool., Havv., Cambridge 121: 371-496, pls. $1-36$.
Williams, A. 1948. The Lower Ordovician Cryptolithids of the Llandeilo District. Geol. Mag., Lond. 85: 65-88, pl. 6.
C. P. Hughes, B.Sc., Ph.D., F.G.S.

